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MICHIGAN ACADEMY OF SCIENCE ARTS AND LETTERS

VOLUME XVII

CONTAINING PAPERS SUBMITTED AT THE ANNUAL MEETING IN 1932

(This volume contains papers in Botany, Forestry, and Zoölogy only. Volume XVIII will contain papers in Anthropology, Economics and Sociology, Geography, Geology and Mineralogy, History and Political Science, Language and Literature, Mathematics, and Psychology.)

PAPERS

OF THE

MICHIGAN ACADEMY OF SCIENCE ARTS AND LETTERS

EDITORS

EUGENE S. McCARTNEY
UNIVERSITY OF MICHIGAN

PETER OKKELBERG
UNIVERSITY OF MICHIGAN

VOLUME XVII

"Pusilla res mundus est nisi in illo
quod quaerat omnis mundus habeat."
— SENECA, *Naturales Quaestiones*

Ann Arbor
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AN ACKNOWLEDGMENT

ELEVEN years ago the manuscript for Volume I of this publication was submitted to the Graduate School of the University of Michigan for preparation for the press. At that time six sciences were represented. The task of editing would have been an arduous one for a scientist of wide attainments, but for me, a classicist by training, it was a real ordeal. As difficulties were surmounted new problems were presented by the addition of a second annual volume and by the organization of new sections of the Academy. In spite of obstacles improvements were made until eight volumes had appeared.

When Volumes IX and X went to press Mrs. Alice Foster began to read proof for the Plimpton Press. Before I had finished work on the first installment of galley proofs, which contained a long paper of my own, I knew that a person of rare gifts was enthusiastically coöperating with me. I had never seen proof reading raised to so high a plane of scholarship. Since that time her interest and her ardor have never waned. Her devotion to this work is not excelled by my own. Mrs. Foster has never been a reader save in name; she has been a fellow-editor, although the responsibility and the decisions, both wise and unwise, have naturally rested with the official editor.

In volumes of this kind there are always blemishes, some of which represent reluctant concessions of the editor, but his most efficient work amid the intricacies of modern manuscripts is not even suspected unless the reader happens to be also an editor. Technical papers in fields of learning so diverse as those comprised in the Academy volumes create a maze of problems, many of which are difficult of solution. In all these subjects Mrs. Foster has been alert in detecting any lapse from the best form and equally resourceful in suggesting improvements. It is a real pleasure to make an acknowledgment of her unfailing aid.

I wish also to thank the entire staff of the Plimpton Press. For eleven years I have received whole-hearted assistance from its members. Their help and suggestions have always been welcome.

E. S. McC.

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THE CRATAEGI OF GRAND RAPIDS, MICHIGAN, AND VICINITY *

VIRGINIA C. ANGELL

THIS study of the genus Crataegus was begun in September, 1928, at the suggestion of Professor H. H. Bartlett, of the University of Michigan, after it had been found impracticable to identify the Crataegi of Grand Rapids and vicinity by any current key, in spite of the fact that some of Professor Sargent's earliest work (cited later) was based upon Grand Rapids material. Sargent, who subdivided the genus more elaborately than any other investigator, followed the plan of separating species upon very fine distinctions. He first made observations and named his species, and later substantiated his right to call them true species by the contention that they bred true from seed. The greatly enlarged number of species which he and a few other botanists have sponsored has complicated the problem of classification to such an extent that identification becomes an undertaking for only the trained and persistent systematist. We in Grand Rapids have been totally unable to classify satisfactorily any local individuals according to Sargent's key.

The very broad conception of species in older systematic works made it possible to assign names to all specimens collected, but when the material from a wide geographic range of these supposed species was examined it was found in nearly every instance to be a mixture of diverse types. The necessity that existed in 1900 for extensive splitting is not questioned, but the wild orgy of describing as a "species" nearly every individual of which adequate specimens were collected has led to a situation equally impossible.

* Papers from the Department of Botany, University of Michigan, No. 371. The illustrations from photographs and the fruit drawings are contributed by Miss Frances L. Stearns.

Now that the problem has become almost hopelessly involved nomenclatorially, a local student can hardly hope to grapple with it successfully, so far as having any expectation of using the oldest applicable name for each distinguishable type is concerned. It is believed, however, that the local botanists do have an important contribution to make in determining, each for his own area, into how many distinct categories the Crataegi fall if *all* trees are to be placed instead of merely a few outstandingly peculiar ones, such as it has been the recent practice of the specialist to single out for description.

In classifying the Crataegi of Grand Rapids we have followed a plan quite different from that used by Sargent, since we choose to group all individuals examined into a reasonable number of species which may be recognized in the field with a fair degree of accuracy. One should bear in mind that:

1. Attempts to link up these groups of similar individuals with the species listed in the several existing keys have usually brought us to a point where it has seemed necessary to split descriptions and combine portions of them in order to place members of our local groups. Therefore, in Table I, following this discussion, we have chosen to say only that the species which we commonly call by a catch name closely resembles a particular species of Sargent as given in his *Manual of the Trees of North America*,[1] a particular species of Gray's *Manual* (to which Eggleston contributed the treatment of Crataegus), and a particular species as listed by Sargent in his report, *Crataegus in Southern Michigan*.[2] When resemblances were uncertain, we have felt that indicating even a similar species would be unjustified and hence have named no corresponding species.

2. No attempt has been made to prove that our groups come true from seed and therefore are species according to Sargent's conception. It may well be doubted whether Sargent's observations in this regard are dependable.

3. We have not met the problem of permanent naming. We

[1] Houghton, Mifflin and Co., Boston and New York, 1905.

[2] Published by the State Board of Geological Survey as part of the Report for 1906.

use the term "species" to designate groups of similar individuals which we have been able to recognize in the field. Within two of our species we find groups of individuals the members of which, although differing from one another in minor details, are more similar to one another than they are to other individuals of the species. These we designate as varieties. Whenever relationships were clear, although descriptions varied in details, we have used old, established scientific names. For convenience in reference we have employed some common and some pseudo-scientific, non-Latin names, which will, of course, have no nomenclatorial status.

This work was done with the coöperation of Miss Frances L. Stearns in her laboratory at Grand Rapids Junior College; collections were made from areas within the city limits of Grand Rapids and from outside within a radius of about five miles. Our collections include preserved opening buds and inflorescences, pressed spring and fall specimens, formal check records for all structures found to be valuable in attempted classification, preserved fruits, spring drawings, a complete set of fruit drawings, Van Dyke and blue prints, and a series of spring and fall photographs. These have given us working material for final formal descriptions and for a dichotomous key, usable in nearly every instance with either spring or fall specimens.

A definite statement in regard to one group of trees to which we shall refer as *Crataegus mollis*, and which aptly illustrates the situation in regard to any one of the groups presented, may make clearer the scope of this problem and our attitude toward it. In this particular group there is available an old name which has been so broadly used in the past that we may continue to use it for the present without danger of complicating the botanical record. If it had been necessary to extend the definition of one of the finely split species we should have hesitated to do so, preferring, in the present state of our knowledge, to use a "common" name. Sargent's work on the Crataegi of Grand Rapids was based upon the collections and observations of Miss Emma J. Cole, supplemented by his own observations during one visit in 1903. He

described fifteen new species from this vicinity. It will be quite justifiable, eventually, to apply Sargent's names to some of our species, but for the present we prefer to proceed with what may appear to be excessive caution.

Crataegus mollis

The species *Crataegus mollis* is variable by differences so minute and shifting as to make fine subdivision of local material not merely difficult, but wholly unjustified. With the progress of this investigation it has become undeniably apparent that:

1. The classification of Crataegi from ordinary herbarium specimens is an impossibility, owing to the transience of many characters used in classification and to the extreme variability of specimens taken from different locations on a given individual.

2. In a group of three hundred trees of *Crataegus mollis* examined individually no two appeared to be alike within the limits of expected fluctuating variation. At the same time none stood out as being quite distinctly different from all the others. Had we acted only as groupers we should have placed the three hundred trees in one collective species as *C. mollis*. Had we acted as splitters we should have collected, mounted, figured, and keyed three hundred separate and distinct species; for within the species as we present it groups of characters do not appear repeatedly in the same combinations. That is, there are minute characters which may easily distinguish an individual tree from any other. Some of these differences may be found on other specimens, but these features do not appear in groups, fixing several trees as of one kind; instead they appear singly in other individuals. For example, ten distinguishing characteristics for one individual will appear separately on ten other trees differing among themselves and from the original specimen. It is often said by pomologists that no two seedling apples are alike. Every seedling, if of economic value, is potentially a horticultural variety distinct from every other. This may be shown by grafting, which demonstrates the stability and persistence of the minute distinctions which are necessarily used to define the slightly different individual

seedlings. The similarity of the two situations forcefully suggests that the critical analysis of large cultures of seedlings is needed in order to demonstrate the supposed coming-true from seed of the Crataegi.

3. As a primary key character we could not make use of variations in opening buds and bud scales. Although outstanding, characters are not correlated strongly enough to make them the basis for identification. Neither could we use leaves in the bud, inflorescence, or individual flowers or their parts, as other investigators did. The variation of fruits in regard to size and shape from branch to branch and from tree to tree was in many instances apparently because of soil or other ecological conditions. Frequently there was a wide variation in the single inflorescence. Cross-sections of the fruits in *C. mollis* help to distinguish this species from others, but do not distinguish varieties within the species.

4. Leaf variation, although somewhat shifting and, therefore, not easily affording key characters, appears to give a nearer approach to distinguishing varieties within the species. In spite of all that has been said concerning variation within the species *C. mollis*, it is nevertheless true that certain trees do look unlike one another in the field, that certain other trees do look alike, and that the distinction is caused mainly by leaf characteristics and general aspect of growth. The similarity of groups of individuals within the wide limits of the species serves to break the entire species into several varieties. The limits of these varieties are wide enough for a fairly confident placing of individuals by any careful student, although many transitional forms may be expected.

Other Species

A condition similar to that described for *C. mollis* occurs in regard to the greater number of our species, although not all show distinct varieties. We were unable to make use of stamen number and color as points of distinction, since these characters were extremely variable. Instead we found leaf and fruit character to be the deciding features for distinguishing all species except

one or two. An interesting situation occurred in regard to *Crataegus succulenta*, in which, instead of basing varieties upon one character, such as leaf form, as was done in *C. mollis*, we found it necessary to select and use a different characteristic for each variety within the species. The species itself was distinguished by ventral cavities on the inner faces of the nutlets; but fruit size and shape, leaf size, shape, and texture, and period of blooming distinguished the varieties.

We have recognized thirteen species and thirteen varieties of the genus in this study. The order of blooming in our species separates them into three groups which, although overlapping, stand out distinctly. They are an early-, a middle-, and a late-blooming group. *C. mollis* and Crataegus "bronze" start the season and form the early group. *C. mollis* blooms as early as April 29. Both these species are large in bud, leaf, flower, and fruit; both are hairy. C. "bronze" is closely related to *C. mollis*, but is easily distinguished in that its young leaves are thin and hairy, in contrast to the woolly-tomentose leaves of *C. mollis* (Pl. I, Figs. 1–2).

The middle group consists of several species blooming in quick succession. Members of it show similar general characteristics. The leaves are definitely not cuneate at the base, but are oval or ovate and definitely lobed and have medium-sized fruits, in contrast to the large fruits of the early group. Prominent catch features have proved most valuable to use for recognition in the field. Crataegus "cut-leaf," among the first of the middle group, stands out in having leaves distinctly acutely deep-lobed throughout, with one pair of especially deep sinuses just below the middle (Pl. IV, Fig. 17 *a*; Fig. 17). The fruits are distinctly pruinose; the leaves turn rose-colored in autumn. Crataegus "red-calyx" is distinguished in spring by a dark purple-red and green calyx tube, which is long, narrow, and obconic and tapers gradually from the pedicel, and which has long-acuminate, entire, eglandular calyx lobes, wrinkled on the back (Pl. II, Fig. 8). It also shows a conspicuously pyriform, angled fruit (Pl. IV, Figs. 18 *b–c*; Fig. 4 *a*). The tips of the calyx lobes break frequently in maturing, leaving remnants of a triangular shape (Fig. 4 *b*). Crataegus "claw-spine,"

following in the blooming period, shows short, stout, recurved spines, oval, straight-sided leaves (Fig. 19), and mealy, ovoid, edible fruits which ripen early (Pl. V, Figs. 19 *a–c*). Crataegus "woodcliffe" comes soon after. We recognize it by its conspicuously large flowers, glossy, broad-triangular leaves with both sides of the basal sinus curving away from each other (Fig. 20), by its calyx with a basal hip, and by its late-ripening, rose-red fruit (Pl. V, Figs. 20 *a–c*). A closely related species, Crataegus "right-angle," is distinguishable in the field because of its smaller flowers, narrower leaves with approximately equal lobes, one pair of which forms nearly right angles (Fig. 22; Pl. VI, Fig. 22 *a*), the absence of a collar on the fruit, and the green and red mottling in contrast to the rose-red fruits of C. "woodcliffe" (Pl. V, Figs. 20 *a–c*; Figs. 6 *a–b*). Crataegus "dainty," a species resembling C. "claw-spine" and C. "woodcliffe," shows leaves with irregular, sharp, curved, red-tipped serrations, and few secondary veins (Fig. 21; Pl. VI, Fig. 21 *a*). Crataegus "burnt-orange" is outstanding for its leaves, distinctly recurved on the midrib and ruffled on the margin (Pl. I, Fig. 3 *b*; Pl. VII, Fig. 23 *a*; Fig. 23), its inflorescence with bud scales and bracts conspicuously orange-glandular (Pl. I, Fig. 3 *a*; Pl. VII, Fig. 23 *b*), its oblate, angular, green fruit with a collar, and an enlarged calyx with persistent glands (Pl. VII, Fig. 23 *c*; Fig. 9). Crataegus "flabellate," the last of the middle-blooming group, seems to be related to no other species in this vicinity. Its small, glabrous, shining, decidedly broadly flabellate leaves (Pl. VII, Fig. 24 *a*; Fig. 24), vermilion, orange, or yellow three-angled fruit (Pl. VII, Figs. 24 *b–c*; Figs. 10 *a–b*) and shrubby form are always distinctive.

All members of the late group show leaves cuneate at the base, and all lack conspicuous lobing (Figs. 25–28). *Crataegus Crus-galli* has inconspicuous bud scales; the leaves are coriaceous, glabrous, and shiny throughout the season (Pl. VIII, Figs. 25 *a–b*). The fruit is dull red with 2 nutlets (Pl. VIII, Fig. 25 *c*; Figs. 11 *a–d*). *Crataegus punctata* has, in contrast, leaves in the bud pubescent (Pl. I, Fig. 4). In the fall it is set off by large, straight-sided, dull, dark red, wine-colored, brown, or yellow fruits with 3 or 4 nutlets (Pl. VIII, Fig. 26 *c*; Figs. 12 *a–d*). The species *Crataegus suc-*

culenta, in which we have recognized six varieties, ends the season. It shows inner bud scales enlarging with the developing stem to form a deep rosette (Pl. I, Fig. 5). Its fruits have a collar, and except in one species are small (Pl. IX, Figs. 27–28; Figs. 13 *a*, 14 *a*). Distinguishing it from all other species are the ventral cavities on the inner face of the nutlets (Figs. 13 *d*, 14 *d*). Within the collective species *C. succulenta* "nearly smooth" is recognized by its glabrous leaves (Pl. IX, Figs. 27 *a–b*); "hispid" by thin hispid leaves; "shrubby" by its shrubby form and abundant, small, nearly crimson, glabrous, globose, or oblate fruits; "large-fruit" by fruit nearly twice the size of any of the others in the species; "big-bud" by its soft-pubescent leaves (Fig. 28) and elongated cylindrical fruits (Pl. IX, Figs. 28 *b–c*; Figs. 14 *a–b*); and "slow" by large, coarse leaves (Fig. 29) and few abortive fruits. This variety ends the blooming period, coming four or five days after all other bloom is gone.

Several hundred trees were minutely examined in this work. Our permanent standardized records cover one hundred and thirty-five individuals. Records, preserved and dried materials, drawings and photographs have been deposited in the Herbarium of the University of Michigan. If further field investigation is made, or an attempt to determine inheritance relations, these collections will serve as bases for comparisons.

Mr. Bartlett expresses the hope that other local botanists will carry further the study of Crataegus here begun, and that they will at first standardize their procedure (1) by keeping careful phenological records of as many individuals as possible, in order to confirm the feasibility of arranging the types in a definite order of blooming; (2) by classifying in phenological sequence all the plants for which records are kept — not merely a few; (3) by describing entire groups of plants rather than singled-out specimens; and (4) by correlating, if possible, or at any rate comparing, the classification for the new locality with that here recorded for the Crataegi of Grand Rapids.

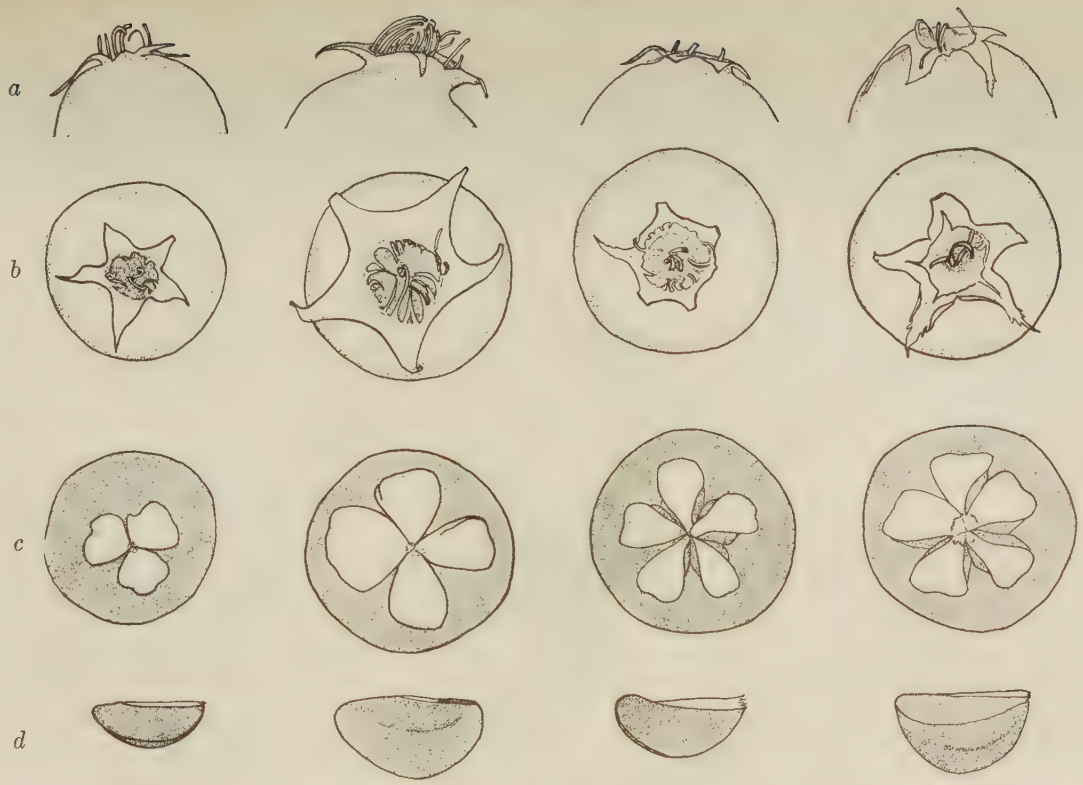
TABLE I

CORRELATION OF THE COMMON NAMES (OF NO NOMENCLATORIAL STATUS) USED IN THIS PAPER WITH MORE GENERAL TREATMENTS OF THE GENUS

Names used in this paper	Gray's *Manual* (Eggleston)	Sargent's *Manual*	Sargent, *Crataegus in Mich.*, based, for the Grand Rapids region, on work of E. J. Cole
1. C. mollis "broad, not lobed"	C. mollis (T. & G.) Scheele	C. mollis Scheele	C. pura Sarg.
2. C. mollis "grape-leaf"	C. mollis (T. & G.) Scheele	C. mollis Scheele	C. pura Sarg.
3. C. mollis "elliptical"	C. Arnoldiana Sarg. or C. submollis Sarg.	C. invisa Sarg.	C. sera Sarg.
4. C. mollis "elliptical, lobed"	C. canadensis Sarg.	C. invisa Sarg.	C. sera Sarg.
5. C. "bronze"	C. Holmesiana Ashe	C. Holmesiana Ashe	.....
6. C. "cut-leaf"	.....	C. bellula Sarg.	C. bellula Sarg.
7. C. "red-calyx"	C. Oakesiana Eggleston	.....	.....
8. C. "claw-spine"	C. macrosperma var. demissa (Sarg.) Eggleston	C. pentandra Sarg.	.....
9. C. "woodcliffe"	C. deltoides Ashe	C. pruinosa K. Koch	C. opulens Sarg.
10. C. "dainty"	C. beata Sarg.	C. georgiana Sarg.	C. Coleae Sarg. or C. honesta Sarg.
11. C. "right-angle"	C. Jesupi Sarg.	C. disjuncta Sarg.	.....
12. C. "burnt-orange"	.....	.....	.....
13. C. "flabellate"	C. aprica Beadle	C. aprica Beadle	C. flavida K. Koch
14. C. Crus-galli	C. Crus-galli Loud.	C. Crus-galli L.	C. Crus-galli L.
15. C. punctata	C. punctata var. rubra Ait.	C. punctata Jacq.	C. punctata Jacq.
16. C. "yellow-punctata"	C. punctata var. aurea Ait.	C. punctata var. aurea Ait.	.....
17. C. "brown-punctata"	C. pausiaca Ashe	C. pausiaca Ashe	.....
18. C. succulenta "big-bud"	C. Chapmani var. Plukenetii Eggleston	C. gemmosa Sarg.	C. gemmosa Sarg.
19. C. succulenta "nearly smooth"	C. Chapmani (Beadle) Ashe	.....	C. flammea Sarg.
20. C. succulenta "hispid"	.....	.....	.....
21. C. succulenta "slow"	C. macracantha var. rhombifolia (Sarg.) Eggleston	.....	.....
22. C. succulenta "large-fruit"	C. macracantha var. succulenta (Schrad.) Eggleston	.....	.....
23. C. succulenta "shrubby"	.....	.....	.....

1. *C. mollis* 2. C. "bronze" 3. C. "cut-leaf" 4. C. "red-calyx"

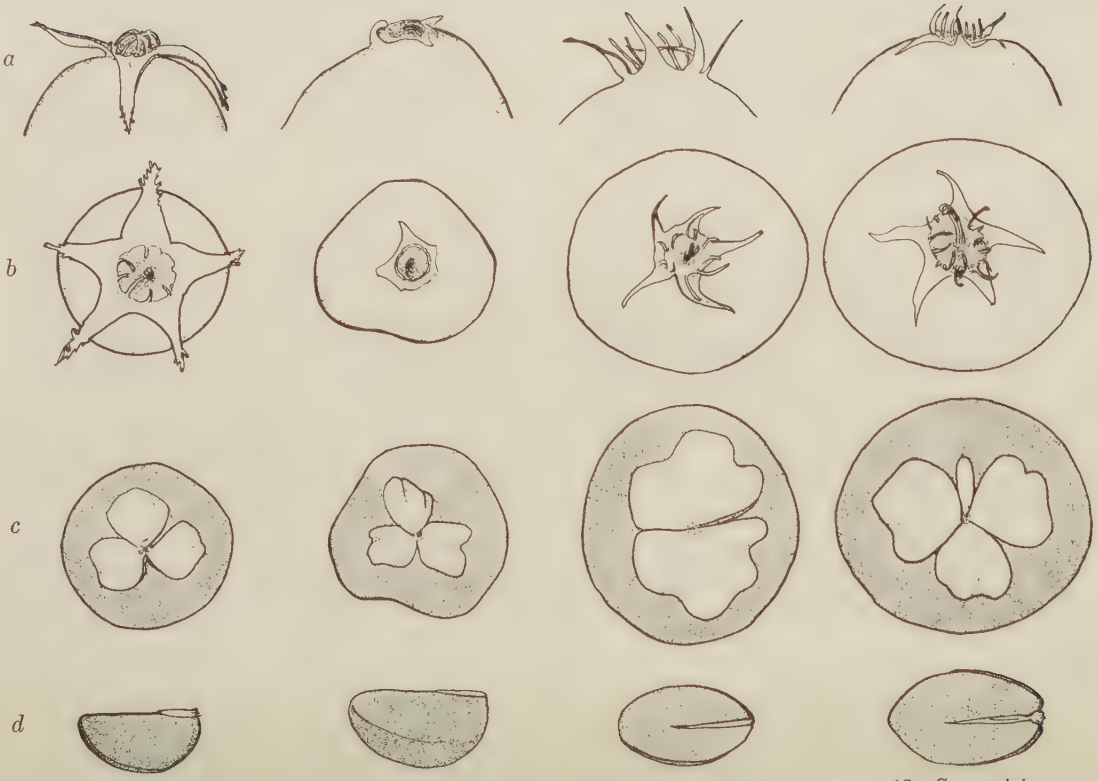
Pomes of Crataegi, showing for each species calyx lobes in lateral and direct aspect (*a–b*), calyx ends cut away to show the nest of nutlets (*c*), and a single nutlet (*d*). Figures are arranged in the order in which the species bloom



5. C. "claw-spine" 6. C. "woodcliffe" 7. C. "dainty" 8. C. "right-angle"

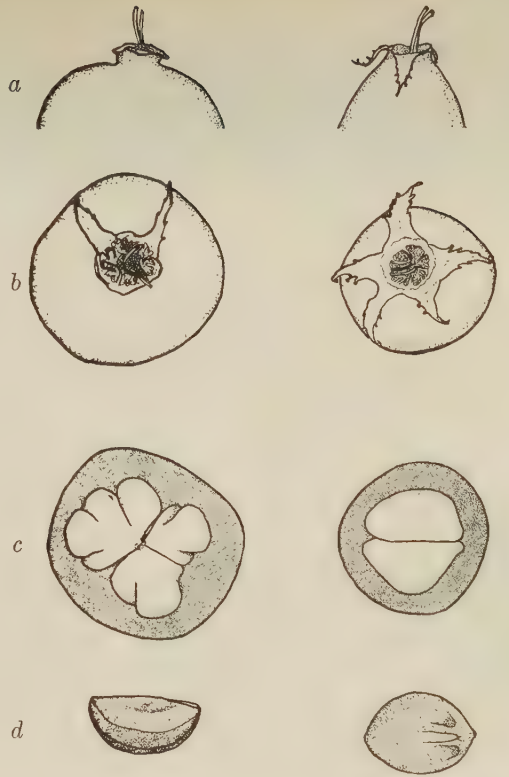
Pomes of Crataegi, showing for each species calyx lobes in lateral and direct aspect (*a–b*), calyx ends cut away to show the nest of nutlets (*c*), and a single nutlet (*d*). Figures are arranged in the order in which the species bloom

FIGURES 9–12



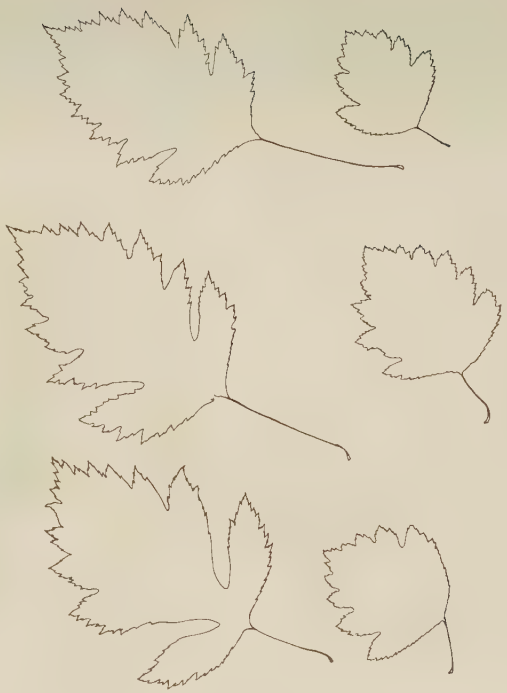
9. C. "burnt-orange" 10. C. "flabellate" 11. *C. Crus-galli* 12. *C. punctata*

Pomes of Crataegi, showing for each species calyx lobes in lateral and direct aspect (*a–b*), calyx ends cut away to show the nest of nutlets (*c*), and a single nutlet (*d*). Figures are arranged in the order in which the species bloom



13. *C. succulenta* "nearly smooth"

14. *C. succulenta* "big-bud"



15. *C. mollis*

Leaves of Crataegi, showing typical forms and range of variation

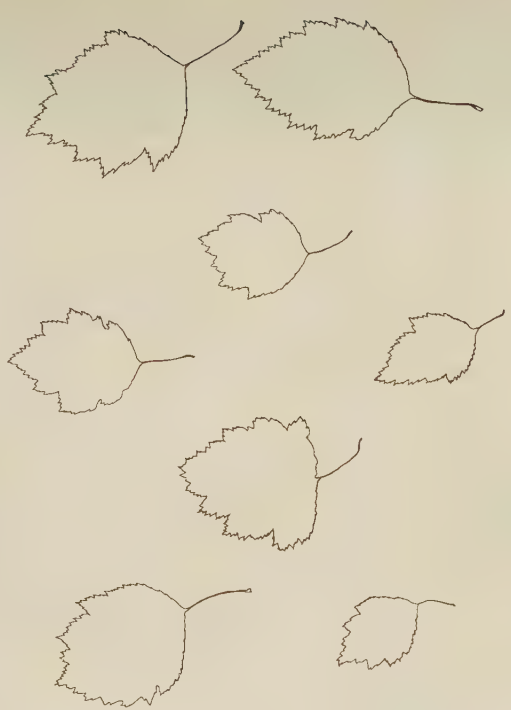
For explanation see page 12

FIGURES 16–17

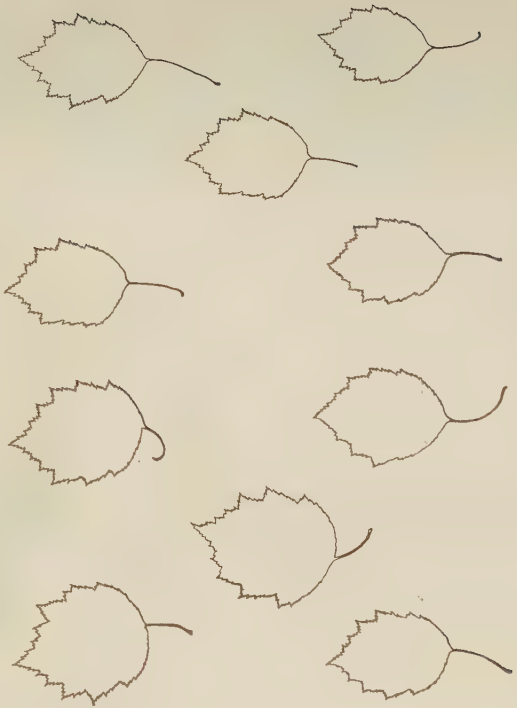
16. C. "bronze"

17. C. "cut-leaf"

Leaves of Crataegi, showing typical forms and range of variation



18. C. "red-calyx"

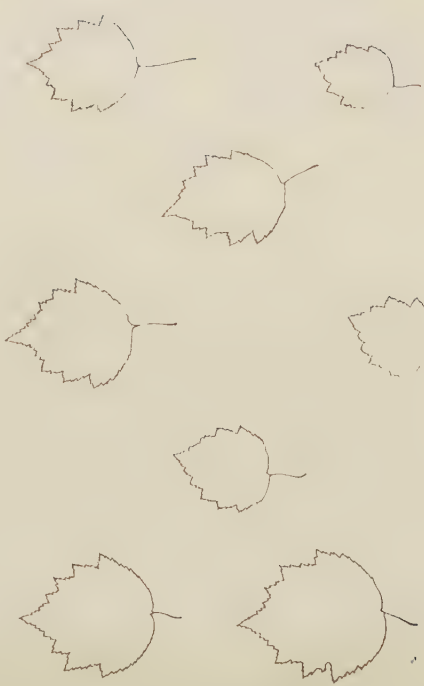


19. C. "claw-spine"

Leaves of Crataegi, showing typical forms and range of variation

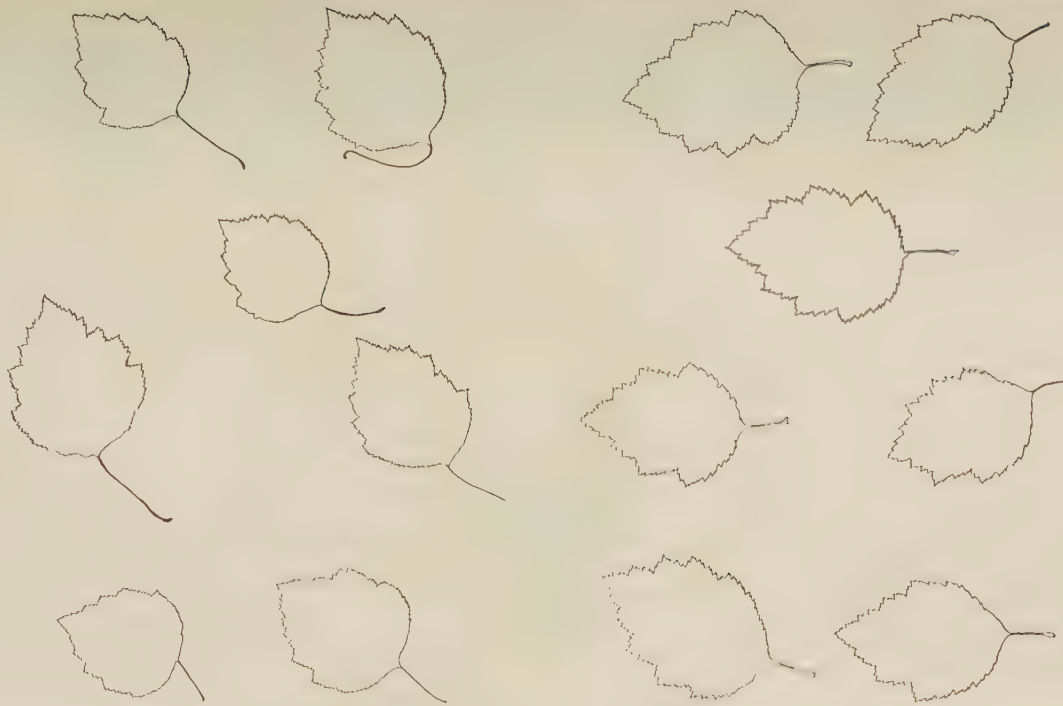
FIGURES 20–21

20. C. "woodcliffe"



21. C. "dainty"

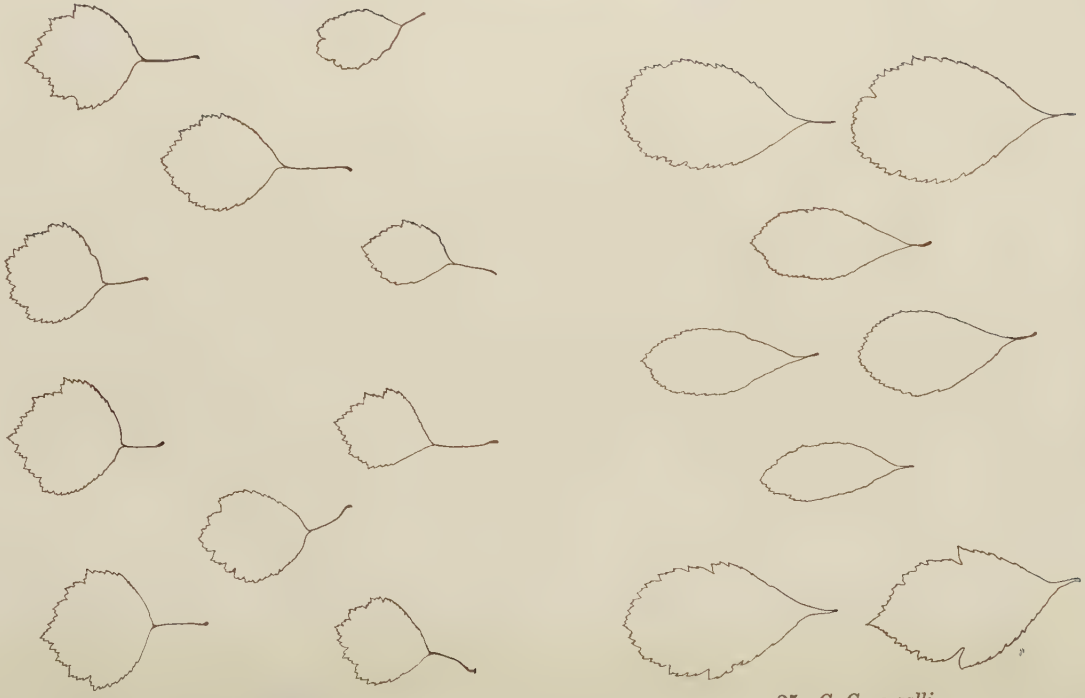
Leaves of Crataegi, showing typical forms and range of variation



22. C. "right-angle"

23. C. "burnt-orange"

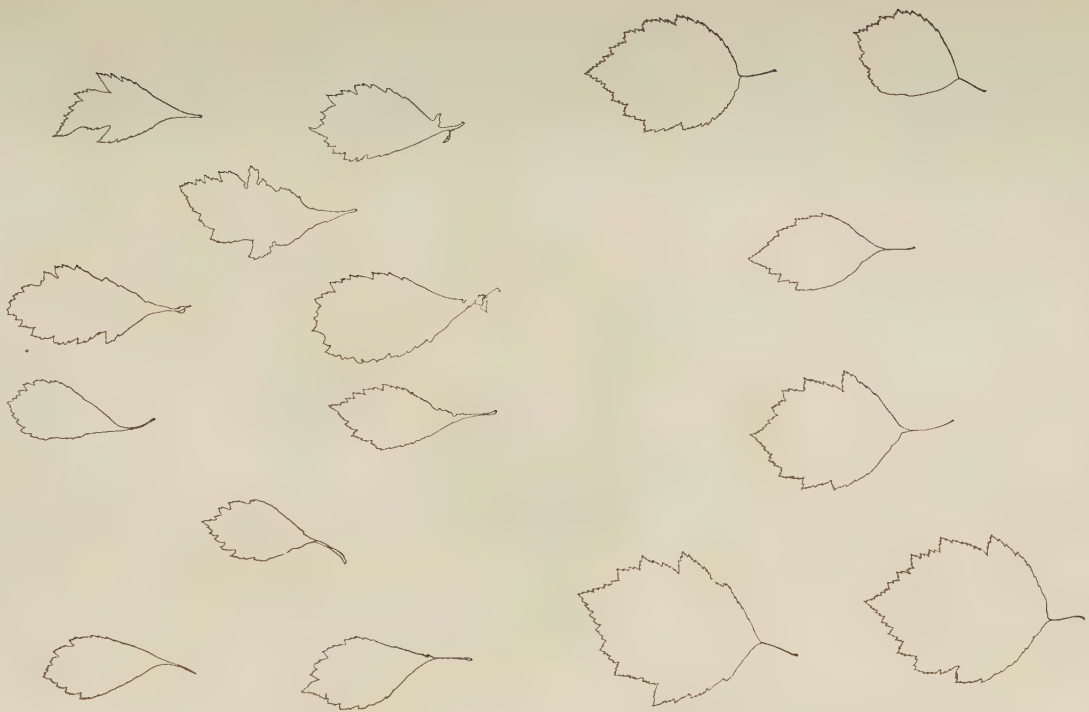
Leaves of Crataegi, showing typical forms and range of variation



24. C. "flabellate"

25. *C. Crus-galli*

Leaves of Crataegi, showing typical forms and range of variation



26. *C. punctata* 27. *C. succulenta* "nearly smooth"

Leaves of Crataegi, showing typical forms and range of variation

FIGURES 28–29

28. *C. succulenta* "big-bud" 29. *C. succulenta* "slow"

Leaves of Crataegi, showing typical forms and range of variation

KEY TO THE SPECIES OR NATURAL GROUPS OF CRATAEGI IN THE VICINITY OF GRAND RAPIDS

A. Leaves on flowering shoots distinctly cuneate at base, obovate, oblong, or oval, distinctly longer than broad, not conspicuously lobed; petioles short, eglandular or nearly so; flesh hard and dry

B. Leaves in bud coriaceous, glabrous; mature leaves shining, dark green; fruit usually oblong; nutlets 2, ridged on the back..... *C. Crus-galli*

B. Leaves not coriaceous, pubescent when young; nutlets 2–4

C. Inner bud scales small, thin, light yellow to brown, early deciduous before unfolding of leaves; leaves in bud pubescent; veins prominent; fruit 1–2 cm. long, short-oblong to obovate, straight-sided, dull dark red, wine-colored, brownish or yellow, collar absent; nutlets 2–5..... *C. punctata*

C. Inner bud scales enlarging with developing stem, broad-ovate, red and light green, forming a deep rosette; fruit shining orange or scarlet, less than 2 cm., oblate to cylindric, collar present, ventral cavity present; nutlets 2–3; flesh succulent.... *C. "succulenta" group*

A. Leaves on flowering shoots abruptly tapering, truncate to cordate at base, not distinctly cuneate or obovate, conspicuously lobed

B. Leaves in bud densely pubescent, woolly in spring; inflorescence many-flowered, stamens 20, white; among the first species to bloom; fruit large, 1–2.5 cm., scarlet, flesh thick, edible; nutlets 5, flat on backs, with deep sinuses, pointed at ends (see p. 24) ..... *C. mollis*

B. Leaves not densely pubescent or woolly in spring; fruit smaller than those of preceding, or if larger, green

C. Leaves distinctly acutely deep-lobed, consistently with one pair of especially sharp sinuses just below middle; base frequently somewhat cuneate; infloresence 4–5-flowered; fruit distinctly pruinose, rose; nutlets 3–5 (4); flesh dry and hard; autumn color distinctly rose..... *C. bellula*

C. Leaves variously lobed

D. Leaves distinctly recurved on midrib, inflorescence and bud scales and bracts conspicuously orange-glandular in spring; bracts persistent when flowers open; tips of calyx lobes in young buds distinctly exceeding size of bud, meeting and twisting above it; petioles distinctly glandular, red, grooved the entire length; fruit green, oblate, with distinct angular hips near the pedicel end; calyx lobes foliaceous, persistent-red, serrate, collar present.. C. "burnt-orange"

D. Leaves not distinctly recurved on midribs, glands white, red, or brown (not orange); fruit red-orange or yellow (not green)

E. Leaves small, glabrous, shining, distinctly broadly flabellate, short, rhombic, or orbicular; corymbs few-flowered; stamens 3–5, frequently abortive; fruit orange, yellow, or vermilion, frequently 3-angled; nutlets 3; flesh dry and hard; a low shrub..... C. "flabellate"

E. Leaves not flabellate, short, rhombic or orbicular; fruit red or green, red-tinged or mottled, not conspicuously 3-angled

F. Calyx tube narrow, lobes distinctly narrow, linear, entire, both dark purple-red, wrinkled on back; fruit light vermilion-scarlet, cylindric and conspicuously pyriform, angled and tapering abruptly into short collar from about two thirds of way up..... C. "red-calyx"

F. Calyx lobes not outstandingly narrow, linear, usually not entire, not dark purple-red, not wrinkled; fruit not outstandingly pyriform

G. Some of spines short (often 2 cm.), stout, recurved dis-

tinctly and angling back from stem; leaves oval, straight-sided; fruit oval-cylindric or somewhat pyriform, flat on pedicel end; flesh salvy-sweet ..... C. "claw-spine"

G. Spines not short, stout and recurved; leaves not straight-sided, oval; fruit not oval

H. Fruit pruinose; leaves glabrous or nearly so

I. Calyx lobes serrate and glandular the entire length; fruit scarlet; bloom slight; leaves rugose ..... C. "dainty"

I. Calyx lobes with few serrations and glands near tip; fruit distinctly pruinose; leaves smooth

J. Flowers 1–3 cm. in diameter; leaves often as broad as long, frequently with sides of the basal sinuses curving away from each other; leaves triangular in outline; fruit oblate, angular, with a collar, pruinose, rose-red; flesh dry, hard ... C. "woodcliffe"

J. Flowers 1–2 cm., leaves oval or ovate; lobes approximately equal in size, collar lacking, color red- and green-mottled .... C. "right-angle"

H. Fruit not pruinose; leaves hairy but not woolly, tomentose as in *mollis* leaves large ..... C. "bronze"

PUNCTATA GROUP

Fruit dull dark red, purple, or brownish ... *C.* "brown-*punctata*"
Fruit dull red or yellow
  Fruit dull red ..... *C. punctata*
  Fruit clear yellow ..... *C.* "yellow-*punctata*"

SUCCULENTA GROUP

A. Leaves and inflorescence smooth ..... *C. succulenta* "nearly smooth"
A. Leaves and inflorescence pubescent
  B. Leaves hispid, thin ..... *C. succulenta* "hispid"
  B. Leaves soft-pubescent
    C. Leaves (10 cm. or more) large, coarse, rhombic; bloom late (June 5–10); fruit often few, abortive ..... *C. succulenta* "slow"
    C. Leaves not 10 cm., not rhombic; bloom about June 1; fruit usually abundant
      D. Fruit distinctly spherical or oblate
        E. Fruit small to 1 cm., shrubby ..... *C. succulenta* "shrubby"
        E. Fruit larger (1.5 cm.).. *C. succulenta* "large-fruit"
      E. Fruit elongated ..... *C. succulenta* "big-bud"

MOLLIS GROUP

A. Leaves broad-cuneate or abruptly tapering at base, distinctly longer than broad, elliptic
  B. Leaves distinctly deeply lobed .... *C. mollis* "elliptical, lobed"
  B. Leaves with short, sharp lobes .... *C. mollis* "elliptical"
A. Leaves broad at base
  B. Leaves on vegetative shoots as broad as long, deeply lobed, teeth long, pointed, curved ..... *C. mollis* "grape-leaf"
  B. Leaves on vegetative shoots orbicular, not conspicuously lobed... *C. mollis* "broad, not lobed"

CHARACTERISTICS COMMON TO ALL VARIETIES OF THE SPECIES *CRATAEGUS MOLLIS*

SPRING BUD

Inner bud scales
- not lobed
- densely glandular on the margins and on the inner surfaces
- with dull sessile glands, white changing to red and brown
- with revolute margins conspicuous
- green and red, often green with a red stripe up the midrib, or light brown

Stem growth
- long when the leaves unfold

Leaves in the bud
- thick and pubescent
- folded on the midrib
- yellow-green

INFLORESCENCE

Bracts
- glandular

Flower buds
- densely pubescent to villose
- with green calyx
- with calyx lobes serrate, glandular-margined with red glands

Flowers
- with petals spreading 1.5–2 cm.
- with anthers 20, white to yellow
- with styles 3–5, predominantly 5

LEAVES

- 4–13 cm. long
- elliptical, narrowly ovate to orbicular, more or less lobed
- sparingly pubescent above when young, becoming nearly glabrous in maturity
- whitish below and nearly glabrous in maturity, but pubescent to densely tomentose below throughout spring and summer months
- membranaceous, thin to thick, but not strictly coriaceous even in maturity
- with stipules lunate or often broad, glandular with red glands, often persistent in maturity, especially on the vegetative shoots

FRUITS

- 1.5–2 cm. long and broad
- globoid or short-oblong or pyriform, often several forms in a single corymb
- scarlet
- pubescent
- with thick yellow flesh

FRUITS (*continued*)

with nutlets 5
nutlets without ventral cavities
calyx lobes persistent or deciduous
calyx lobes glandular-serrate
with pedicels pubescent

Crataegus mollis "elliptical"

Variety "elliptical" is distinguished from the other varieties included in the group by having:

1. Leaves longer than broad;
2. Margins running from slightly lobed to very deeply lobed;
3. Sinuses sharply cut, acute;
4. Stipules conspicuously persistent on the vegetative shoots, lunate, and often enlarged;
5. Calyx lobes tending to rise and hook back;
6. Leaves more or less dished;
7. Young vegetative shoots orange, zigzag.

Other frequent features which help to distinguish this variety are:

1. The two basal lateral veins are not parallel, but somewhat divergent;
2. There may be some leaves on each tree with a pair of sharp deep basal sinuses running parallel with the lateral veins;
3. Young vegetative shoots may have spines and a pair of buds in the axils of the leaves;
4. The fruit may be elongated or round on different trees or on the same tree;
5. The calyx lobes are often deciduous;
6. Heart-shaped bases often mark leaves on the vegetative shoots;
7. Cuneate bases are often found on the vigorous vegetative shoots.

Crataegus mollis "elliptical, lobed"

Variety "elliptical, lobed" may be distinguished in the group given above as having:

1. Leaves deeply lobed;
2. Most of the sinuses running nearly parallel with the secondary veins.

Crataegus mollis "grape-leaf"

Variety "grape-leaf" agrees with variety "elliptical, lobed" except that:

1. The leaves are predominantly broader than long;
2. The margins are sharply doubly serrate with long narrow teeth;
3. Leaves on the vigorous vegetative shoots are always distinctly lobed. (Variety "elliptical" gave a range of slightly to deeply lobed.)

Crataegus mollis "broad, not lobed"

Variety "broad, not lobed" may be distinguished from variety "grape-leaf" in having leaves merely irregularly serrate to very slightly lobed. The broad leaf form is like that in variety "grape-leaf," but the absence of lobing is conspicuous

Herbarium specimens 57, 64, 65, 80, 82, 93, 94, 126, 130.

Illustrations: Pl. I, Figs. 1, 6; Pl. II, Figs. 15 *a–c*; Pl. IX, Figs. 29 *a–d*; Fig. 15. A series of blueprints of leaves of the varieties of this species accompanies the herbarium material.

Crataegus "bronze"

A large shrub of irregular contour, or a tree 10–15 feet tall, with a short trunk, spreading in the open into a broad, symmetrical head. Young growth at the top of the tree of coarse appearance, vigorous, contorted, knotty, owing to the growth of many small branches bearing flowering shoots. Young twigs shining, light red-brown, with conspicuous dull white lenticels; old twigs smooth, gray, stout. Spines 2 5 cm. long, usually 4–5 cm., stout, straight or slightly curved at the point, this year's red-brown, becoming darker brown and gray, few. Winter buds globular, 2–4 cm. long; outer bud scales coriaceous, glabrous, broad-ovate, keeled, with acute tip, frequently apiculate, entire or with a few serrations or lobes, light brown to red-brown; inner scales membranaceous, glabrous, entire, moderately to densely glandular on the margins with sessile, short- or long-stipitate, dull, white, red, or brown glands; on the surfaces eglandular or with few glands, in some forms densely glandular; position erect, recurved, or spreading; deciduous after the leaves unfold; enlarging to 2 cm.; green or red, or green with light red tip. Stem growth long when the leaves unfold. Inflorescence 5–19-flowered, more in some trees. Pedicels 1–2 cm. long, hairy. Bracts linear, lunate, glandular. Flowers opening with the leaves. Flower buds ovoid to globose or only slightly flattened, green tinged with red, sparsely pubescent. Calyx tube cylindric, obconic, or slightly turbinate; lobes narrow, red-tipped, with broad sinuses; margins serrate, glandular, with dull red glands. Calyx lobes keeled. Petals 1.5–2 cm. long, smooth-margined or slightly cupped, spreading, white. Stamens

fewer than 10; anthers dark pink, full. Styles 3-5. Leaves in the bud pubescent above with short, straight, rough, white hairs; thin, folded on the midrib and plicate, ruffled, bronze, distinctly recurving. Stipules present, early deciduous, linear to broadly ovate; some lunate with a basal division; stipitate-glandular-margined. Summer color dull, dark green above, whitish below. Mature leaves 4-10 cm. long, ovate and broad-ovate or oblong, distinctly lobed with broad, shallow lobes and acute or obtuse sinuses. Leaves of the vegetative shoots often with a pair of deep basal sinuses and several sinuses with both sides curving away from each other, coarsely serrate or irregularly doubly serrate to the acute or acuminate tip, with long teeth; bases mostly clearly unequal, few tapering abruptly, mostly truncate or distinctly cordate; veins conspicuous below. Leaves glabrous above and below except for minute pubescence along the veins, subcoriaceous or almost coriaceous. Petioles glandular, frequently wing-margined on the vegetative shoots; grooved the entire length. Fruit 1–1.5 cm. long, 1–1.5 cm. wide, globoid to cylindric, sometimes slightly angled, concave at the pedicel end. Pedicels 1 2 cm. long, very sparingly pubescent. Calyx lobes persistent or deciduous, as large as the fruit, long and narrow, twisted, flat or with a slight collar, red, serrate, with a few hairs persistent. Fruit scarlet to vermilion-scarlet, glabrous, with a slight bloom; lenticels conspicuous; flesh thick, yellow, mealy. Seeds 3–5, ridged or grooved, flat on the inner faces; sinuses shallow or deep. Common in rich upland pastures, but almost entirely lacking along the river flood plains. A typical individual may be located across from the roadside rock garden at Ravenswood, in the east end of the city on the property beyond the Wegge residence. The property is now a part of the Paris addition. Several mature specimens are to be seen in the wooded area. Herbarium specimen 5 A. Pl. I, Fig. 2; Pl. II, Figs. 7, 11; Pl. III, Figs. 16 *a–c*; Figs. 2 *a–d*, 16.

Crataegus "cut-leaf"

A large shrubby form, or a tree 10–15 feet tall, spreading into a flat top at about 5 feet. Terminal branchlets outstandingly

twiggy, contorted. Trunk gray-brown, dull orange in the fissures; young branches shining brown. Spines usually 3–5 cm. long, frequently 5–7 cm. long on vigorous young plants, straight or slightly curved; spines of the year light red-brown, becoming darker brown and gray, few or many. Winter buds globular, 2–4 mm. long; scales coriaceous, glabrous, short and broadly ovate, keeled slightly or not at all, rounded or apiculate at the tip, margins entire; color bright dark red to brown. Inner bud scales enlarging with the developing stem, membranaceous, entire or serrate, margins moderately glandular with sessile or stipitate red or white glands; surfaces not glandular; position spreading or recurved, the margins flat; color light brown or yellow-brown. Scales mostly deciduous before the leaves are entirely unfolded. Inflorescence with 4–5 flowers on pedicels 1.5–2 cm. long, opening as the leaves are nearly unfolded. Bracts of the inflorescence linear, lunate, glandular, mostly deciduous at the time of bloom. Flower buds cylindric to globose and flattened, green, glabrous. Calyx cylindric to slightly obconic and turbinate, of medium length. Calyx lobes very slightly red-tipped, narrow- or broad-triangular with few serrations, sparsely glandular with white or dull red, short-stipitate glands; slightly keeled; tips of the calyx lobes lying on the buds, not meeting, and twisting above the petals. Petals white, full, and ruffled or smooth-margined, slightly cupped, erect or flat; spread of the petals 1.5–2 cm. Stamens 10 or fewer than 10; anthers dark red, red or pink, full or shrunken. Styles 3–5. Leaves in the bud glabrous, thin, folded on the midrib and plicate, yellow-green; position erect, becoming horizontal and sometimes slightly recurving; deep acute sinuses running parallel with the secondary veins apparent in the juvenile forms. Stipules early deciduous, linear, lunate, lobed, some with basal division, glandular-serrate. Mature leaves 4–8 cm. long, ovate and oblong-ovate, doubly serrate on the lower half and serrate to the acute or acuminate tip; bases mostly equal, abruptly tapering to cuneate, infrequently truncate; leaves distinctly and deeply lobed, the basal lobes, especially, often cut three fourths of the distance to the midrib; sinuses acute, running parallel with the secondary veins; in many leaves the basal

sinus, especially, is narrow; veins conspicuous below, leaves glabrous above and below, very slightly rough in some cases, membranaceous. Petioles more or less glandular, grooved from one half to the entire length, very slightly or not at all wing-margined. Stipules early deciduous. Summer color above, light to dark green, dull; below, whitish. Leaves not flat, slightly dished, slightly recurved on the midrib; foliage standing up from the twigs and twisting in all directions. Autumn color a distinct and beautiful rose. Fruit 1.5–2 cm., long and broad, globoid or oblate, somewhat angled; flat or conical on the pedicel end. Pedicels 1–2 cm., glabrous. Calyx red or green, persistent or deciduous, not so large as the fruit, erect with a slight collar. Lobes narrow to slightly broad-triangular, with a few teeth or often three-lobed at the tip, glabrous; lenticels conspicuous. Fruit rose-colored, glabrous, with abundant bloom; flesh green. Nutlets 3–5, mostly 4; ridged or grooved; ventral cavities absent; sinuses not deep, nest of nutlets 8 mm. high, 10 mm. wide. Frequent in rich pastures. A typical specimen may be found in the hedgerow of the first crossroad running parallel to M-16, about one mile east of the Ridgemore Country Club on the same road. It is within 150 feet of the road in the line of trees along the old rail fence. Herbarium specimen 17. Pl. II, Fig. 12; Pl. IV, Figs. 17 *a–c*; Figs. 3 *a–d*, 17.

Crataegus "red-calyx"

A wide-spreading symmetrical tree growing to about 12 feet in height; trunk short; very leafy and rich in appearance, foliage entirely concealing the twiggy branches. Young twigs light brown, older ones dark brown to gray. Spines 3–4 cm., straight or slightly curved, light red-brown becoming gray, few. Winter buds globular, 2–4 mm., shining red-brown; scales coriaceous, glabrous, entire, broadly ovate, keeled, acute, barely apiculate. Inflorescence 5–10-flowered, a few with more than ten. Pedicels 1.5–2 cm. long, glabrous. Bracts linear, minutely glandular, deciduous before the opening of the flowers. Flowers appearing with the leaves. Flower buds ovoid to globose, broad and flattened, glabrous, green and dark purple-red. Calyx tube long, narrow, obconic,

tapering gradually from the pedicel. Calyx lobes narrow, with broad, rounded sinuses, entire, eglandular, without keel, wrinkled on the backs of the lobes; tips of the lobes red. Petals spread from less than 1 cm. to 1.5 cm., smooth, full or slightly cupped; erect and spreading; white. Stamens about 10, dark pink to dark red or rose, full. Styles 3–5. Leaves 4–7 cm. long, ovate or oval, straight-sided or a few oblong; distinctly but not deeply lobed, serrate or irregularly doubly serrate, with long teeth, many curving out and downward; tips acute or a few acuminate. Bases mostly equal, slightly rounded, tapering abruptly, entire for 1–2 cm. from the petiole; veins conspicuous below. Leaves glabrous above and below, membranaceous to subcoriaceous. Petioles grooved from one half to the entire length, not wing-margined, not glandular. Stipules early deciduous, linear, glandular-serrate, some with basal division. Summer color above, deep green to light olive-yellow-green; lighter below. Autumn color yellow, pink, orange, and crimson. Fruit 1–1.5 cm. long, 1–1.5 cm. wide; cylindric and conspicuously pyriform; angled and tapering abruptly into the short collar from about two thirds of the way up; flat at the pedicel end. Collar sometimes lacking. C. "red-calyx" has the most distinctly pyriform fruits found on the members of the genus in this community. Pedicels 1–2 cm., glabrous. Calyx not persistent or rarely persistent. Lobes long, narrow, and twisting on the end, glabrous, entire, as large as the fruit; flat, recurved, or erect. The tips of the calyx lobes break frequently in maturing, leaving calyx lobes of a triangular shape. Fruit clear vermilion-scarlet; glabrous but with a slight bloom; flesh yellow to green, sweet, mealy. Nutlets 3–5, ridged or grooved on the backs, flat on the inner faces, ventral cavity absent; sinuses narrow, deep or shallow. Rare in hillside pastures. Typical specimens may be seen in the hillside pasture to the east of Reed's Lake, about one hundred feet from the road. Herbarium specimen 1. Pl. II, Fig. 8; Pl. IV, Figs. 18 *a–c*; Figs. 4 *a–d*, 18. The distinguishing characteristics of C. "red-calyx" are as follows:

Petioles not glandular;

Flower buds dark purple-red on the calyx tube and lobes, in addition to green;

Calyx tube long, narrow, obconic, tapering gradually from the pedicel;

Calyx lobes narrow, acuminate, entire, eglandular, without keel, wrinkled on the back;

Stamens about ten, dark pink to dark red or rose;

Fruit cylindric and conspicuously pyriform, angled in to the short collar from about two thirds of the way up;

Lobes of calyx, when persistent, long-acuminate and twisted on the ends;

Fruit vermilion-scarlet, mealy, edible.

Crataegus "claw-spine"

A shrubby form growing to 9 feet tall, usually about 4–6 feet, irregular in contour, scraggly, somewhat twiggy, but twigs not so contorted as in *C. bellula*. Spines many, ranging from under 2 to 6.5 cm., the short ones stout, blunt, frequently angled on the tips, distinctly recurved; the long ones slender, long-pointed, straight or slightly to distinctly curved. Color light brown, red-brown to dark brown, often dark-tipped, becoming gray. Lenticels small, inconspicuous, lens-shaped, yellow, slightly raised. Outer bud scales dark or light brown, glabrous, entire or lobed; coriaceous; broad-ovate and rounded on the tips or less frequently acute or apiculate. Inner bud scales membranaceous, glabrous, entire or with few serrations at the base, moderately glandular on the margins with sessile or short-stipitate, dull red or white glands. Surfaces of the scales with glands few or none, resinous when glandular; position erect, spreading, and recurved; margins flat; scales mostly persistent until after the leaves unfold, but some deciduous before unfolding of leaves; enlarging to 2 cm., light brown, yellow-brown, red-brown, or more frequently green with light red or pink. Stem growth long when the leaves unfold. Inflorescence 5–10-flowered, frequently a few more or less. Pedicels usually about 1 cm., some reaching 1.5 cm. Bracts linear, a few lunate, resinous with sessile glands. Flowers opening with the leaves. Flower buds ovoid or globose, green or slightly red- or bronze-tinged, glabrous. Calyx tube angled, slender, usually cylindric, often obconic or turbinate. Calyx lobes narrowly tri-

angular with acute sinuses, reflexed distinctly, even somewhat in the bud. Tips acuminate, margins entire or with few serrations, and few dull red or white red-tipped glands. Calyx keeled slightly or not at all. Petals white, spread 1–1.5 cm., smooth or cupped. In some plants there are poorly formed flowers resembling kernels of pop corn, and some flowers that do not open at all. Normal position of petals flat, erect, or spreading. Stamens fewer than 10, rarely 15, pink, deep pink, or red; on some trees full, on others almost no anthers formed, or many anthers abortive. Styles 2–4. Leaves in the bud pubescent, with a few short, white, straight, appressed hairs above; thin; folded on the midrib and plicate; yellow-green or slightly medium green, some with bronze, orange, or burnt-orange tints and red midrib; position erect, horizontal, or recurving. Petioles hairy. Stipules present; linear, lunate, or with basal division; entire or glandular-serrate; early deciduous. Mature leaves 4–8.5 cm., oblong, oval, ovate to nearly orbicular on the vegetative shoots; distinctly lobed with three or four pairs of lobes; serrate and doubly serrate, teeth red-tipped; bases mostly oval, some tapering abruptly, few cuneate; equal or unequal; tips acute or acuminate; sinuses acute, straight-sided, making almost right angles, shallow to medium; veins conspicuous below; surface above, glabrous or very sparsely pubescent; texture membranaceous. Petioles sparsely or not at all glandular on the flowering shoots, glandular on the vegetative; a few hairs persistent; grooved from one half to the entire length; very slightly wing-margined on the vegetative shoots. Stipules early deciduous. Foliage dark green to light green, lighter below or whitish. Leaves flat, petioles not elongated, only slightly recurved. Fruit 1–1.5 cm. long, 0.5–1 cm. wide; cylindric, some approaching pyriform; flat or less often conical or slightly concave at the pedicel end. Pedicels 1–3 cm. long, glabrous. Calyx persistent or often deciduous; often as large as the fruit; position distinctly erect, flat, or recurving and clinging to the fruit. Collar entirely absent. Red color in the calyx little or none. Lobes glabrous, nearly entire, triangular. Fruit color rose and vermilion-scarlet; lenticels not conspicuous; pubescence on the fruit wanting; bloom abundant or slight; flesh thin to

thick, mealy. Nutlets 2–4, rounded on the back or ridged or grooved; flat on the inner faces; ventral cavity absent. Nest of nutlets 5 6 mm. high, 6–7 mm. wide; sinuses absent or shallow. Common on dry ground along roadsides or in upland pastures. Typical individuals may be seen in the valley just north of Perkin's fruit farm, on the crossroad between Knapp and East Leonard. Herbarium specimen 8. Pl. V, Figs. 19 *a–c*; Figs. 5 *a–d*, 19.

Crataegus "woodcliffe"

A tree 12–15 feet high, broad and rounded, with drooping branches, the lower reaching to the ground and concealing the trunk; vigorous, clean-looking, with bright green, very smooth foliage, and decided coppery red tints persistent in the vegetative shoots and leaves around the inflorescence when the flowers bloom. In summer, rich, leafy in appearance. Generally found in dry upland pastures. Twigs with conspicuous, light, lens-shaped, vertical, raised lenticels; conspicuously zigzag on the vigorous olive-green to orange-brown vegetative growth. Outer bud scales dark red, glabrous, coriaceous, broad-ovate; entire, rounded or apiculate at the tip. Inner bud scales glabrous, membranaceous, broad-ovate; the innermost leaflike scales moderately to densely glandular on the margin, serrate at the base with very long-stipitate, red or white, clear or dull, glands; thus the margin appears laciniate; glands on the surfaces few, resinous; position spreading or recurved, with margins flat; enlarging with the developing stem to 2 cm.; deciduous after the leaves unfold; color green with light red variously distributed on the scales, or green with a red midrib broadening into a red triangle at the tip. Stem growth conspicuously long when the leaves unfold. Inflorescence clean, healthy in appearance. Flowers 5–10, opening with the developing leaves. Bloom profuse, flowers large. Bracts linear or lunate; green and red, conspicuously glandular with stipitate, dull, white or red glands. Many of the bracts persistent until the flowers open. Flower buds ovoid to globose; green, frequently tinged with red; glabrous. Calyx tube short and broad, obconic or cylindric, usually turbinate. Calyx lobes broadly triangular, forming a star; abruptly acuminate; entire,

or with few delicate white serrations at the base of the lobe, or with a group of serrations just back of the tip; sparsely glandular on the margin with short-stipitate, dull red glands. Lobes often red-tipped, distinctly keeled, with a conspicuous angular hump at the base of the lobe. Flowers large; petals white, spreading 1.5–3 cm. across; position flat; individual petals flat or slightly cupped or ruffled. Throat of calyx yellow to deep salmon pink. Stamens 20, light pink, full, conspicuous. Styles 3–5. Leaves in the bud glabrous or with very few hairs above; thin, slippery in texture; folded on the midrib; yellow-green or bright medium green with conspicuous, red, bronze, or red-bronze tints persisting when the flowers bloom. Position in the mature bud distinctly horizontal. Leaves triangular in outline even in the developing stages. Stipules linear or slightly broader, lunate, lobed, bright dark green with red midrib, stipitate, glandular with green glands on margin and surface. Mature leaves 4–7.5 cm. long, the vegetative being conspicuously larger and broader than the flowering. Leaves on the flowering shoots vary in fairly constant proportion around 2.5 cm. in width and 4 cm. in length; on the vegetative shoots, around 5.5 cm. in width and 6 cm. in length. Leaves oval, ovate, broad-ovate to orbicular. The orbicular leaves are almost entirely on the vegetative shoots, but some broad and some fan-shaped leaves appear on the flowering shoots. The broad leaves are broadest near the base, giving a triangular outline, and are frequently broader than long. Margins serrate or doubly serrate, distinctly lobed with two or three pairs of lateral lobes; the lowest pairs of lobes on the vegetative shoots are frequently like the basal lobes on C. "burnt-orange," with the upper and lower sides of the sinus curving away from one another; bases equal or unequal; a few cuneate, many abruptly tapering; on vegetative shoots frequently truncate to slightly cordate; some leaves like those characterizing C. "grape-leaf," a variety of *C. mollis,* appear on nearly every one of these C. "woodcliffe" trees; tips acute, infrequently slightly acuminate; sinuses of medium depth, mostly acute, or approaching a right angle, a few obtuse; veins conspicuous below; surface glabrous above, infrequently with few hairs in the axil of the veins below at the base;

texture membranaceous to subcoriaceous. Petioles sparsely glandular on the flowering shoots, glandular on the vegetative shoots; frequently long, recurved distinctly, giving the leaf a horizontal position and exposing the pruinose fruits conspicuously. Leaf blades slightly recurved, flat, or somewhat dished. Fruit globoid or obovoid, infrequently oblate; angled at the calyx end; flat at the pedicel end. Pedicels 1–2 cm., glabrous. Calyx conspicuous, glabrous, margins of lobes entire or with few serrations, persistent or sometimes deciduous; calyx as large as the fruit or slightly smaller; erect or flat; sometimes recurved on the tips; collar slight. Lobes not red, or with a faint reddish tinge under the lens; narrow or broad but triangular; tapering abruptly from the base or sometimes with acuminate tip; sinuses broad. Fruit glabrous, with abundant bloom. Nutlets 4–5; grooved or ridged and grooved on the back; flat on the inner faces; without ventral cavity; nest of nutlets 5–6 mm. high, 7–8 mm. wide. Free fruiting with the fruit well exposed and conspicuous by the recurving of the petioles. This leaf position puts the fruits into prominent view. They hang so that the conspicuous calyx is facing the observer, and with their distinct glaucous bloom against the darker green of the foliage make the tree distinguishable in a group seen from a distance. Autumn color dull red- and green-mottled. Flesh medium thick, green. Several mature specimens may be found in the woods opposite Woodcliffe in East Grand Rapids. Herbarium specimen 10 A. Pl. V, Figs. 20 *a–c*; Figs. 6 *a–d*, 20.

Crataegus "dainty"

A large shrubby form or a small tree with slender branches and a delicate appearance; found on river flood plains or in dry upland pastures. Spines range 3 5 cm. long, slightly curved, stout; brown, red-tipped, many. Outer bud scales light brown, glabrous, broad-ovate, rounded at the tip or apiculate, fringed on the margins. Inner bud scales green and light red, membranaceous, entire, moderately glandular with dull red, sessile glands; surfaces with a few resinous glands; margins flat, scales spreading or recurved. Stem growth long when the leaves unfold. Inflorescence more than 10-flowered, glabrous. Bracts linear,

glandular-stipitate, and shorter than the smooth green calyx which is obconic. Flower buds globose. Calyx lobes narrow, acuminate, red-tipped with dull red glands; sinuses broad at the base, keeled. Stamens 20, pink. Styles 5. Leaves in the bud finely pubescent above and below, yellow-green and bronze, thin, folded on the midrib, and plicate; position erect. Mature leaves with 4–5 shallow lobes, and irregular, sharp, curved, red-tipped serrations; ovate and broader, but mostly longer than broad, slightly cuneate at the base, acute at the apex, glabrous; secondary veins few, impressed above. Surface of the leaf rugose, texture membranaceous. Petioles long, wing-margined on the vegetative shoots, some glandular; in the young leaves pubescent; grooved one half, entirely, or not at all. Stipules a few, persistent, serrate to the tip, linear, lunate, some broader than long, glands persistent. Older leaves dull, dark green to olive-green, lighter below. In autumn the leaves are thick and firm and turn a rose color. Fruit about 1.5 cm. in length, 1.5 cm. wide; globoid, ovoid, cylindric or pyriform, and angled; color scarlet, surface glabrous, without conspicuous lenticels. Bloom slight to abundant. Calyx persistent, sometimes deciduous, sometimes as large as the fruit, flat or recurved, minutely serrate, narrow. Collar slight. Flesh thick and yellow. Nutlets 5, ridged or grooved; sinuses wide, deep; ventral cavities absent. Frequent in rich, moist woods. A typical specimen may be found across from Woodcliffe on Lake Drive in the woods which are now a part of the Paris addition. Herbarium specimen 9 A. Pl. II, Fig. 9; Pl. VI, Figs. 21 *a–c*; Figs. 7 *a–d*, 21.

Crataegus "right-angle"

A symmetrical tree 10–12 feet tall, of ovate or rounded contour, spreading radially by curving of the horizontal branches which arise some four feet from the ground; often with several trunks angling gently, but giving the appearance of one tree. Mass appearance of heavy foliage with branches not outstanding. Winter buds about 2 mm. long, shining, light red-brown; globular; scales closely appressed. Spines 3–6 cm.; young, purple-red; old, gray; straight or slightly curving; stout or slender; medium in number. Lenticels on the twigs vertical, lens-shaped, small,

brown, inconspicuous. Outer bud scales in the opening bud coriaceous, glabrous, broad-ovate, rounded on the tips or a few keeled and apiculate. Inner bud scales membranaceous, glabrous; bright green with a bright, light red midrib; keeled at the tip; margins entire or few-lobed, moderately glandular with short-stipitate or sessile, clear white, red, or brown glands. Inner scales spreading or recurved, margins flat; deciduous after the leaves unfold. Stem growth long when the leaves unfold. Inflorescence about 10 flowered, flowers and leaves opening approximately together. Pedicels 0.5–1.5 cm. long, glabrous. Bracts linear, glandular. Flower buds globose, green, glabrous. Calyx tube slender, of medium length, obconic, and turbinate. Calyx lobes triangular with narrow to slightly broad sinuses; eglandular or with a few glandular-tipped serrations at the base; glands white becoming red and dull; they are minutely red-tipped, strongly reflexed, glabrous, keeled. Petals spread 1–2 cm., mostly cupped, mostly spreading, a few erect or flat; color white. Stamens fewer than 10, dark pink-purple to dark red, full. Styles 3–5. Leaves in the bud erect, recurved, or spreading horizontally; glabrous or minutely hairy with a few hairs on the base of the midrib above; thick; folded on the midrib and plicate; color bright medium green, bright red or bronze, still distinctly tinted when the flowers bloom. Stipules present, linear, lunate, some with a basal division, glandular-serrate with red glands. Mature leaves 4–6 cm. long, ovate and broad-ovate, mostly straight-sided, widest at the lowest lobe, at about one third of the length of the leaf, one of the lower two or three sinuses frequently almost making a right angle. On the vegetative shoots leaves are often nearly round; a few are broader than long. Leaves with 3–5 pairs of medium to shallow lobes; serrate and doubly serrate to the tip, serrations red-tipped; bases unequal or a few equal, tapering abruptly or a few cuneate; on the vegetative shoots truncate or very slightly cordate. Leaves on the vegetative shoots frequently with the sides of the basal sinuses curving away from one another. Tips acute; sinuses acute except the one forming almost a right angle; veins conspicuous below; leaf surface glabrous above and below except for a few occasional

hairs at the base of the midrib above; texture membranaceous. Petioles sparsely glandular on the flowering shoots, glandular on the vegetative, and distinctly recurving; grooved from one half to the entire length, not wing-margined. Stipules early deciduous. Summer color above, dark blue-green to rusty yellow-green, dull; below, light green to yellow-green. Autumn color dull yellow-green, rusty and lighter below. Fruit abundant; 1–1.5 cm. wide and long, obovoid, somewhat pyriform, angled, flat or conical on the pedicel end. Pedicels 1 2 cm., glabrous. Calyx persistent or rarely not persistent, usually not so large as the fruit; position flat. Collar absent. Calyx lobes narrow, glabrous, red, with a very few serrations on the margin; tips acuminate when persistent. Fruit wine- and rose-tinted and green-mottled, with conspicuous lenticels; glabrous; bloom usually abundant; flesh thin to thick, green, mealy, and juicy. Nutlets 3–5, grooved, ridged, or grooved and ridged on the back; sinuses broad; nest of nutlets 5 mm. wide, 6 mm. high, pointed on the ends; ventral cavities absent. Frequent in upland pastures. A typical specimen may be found on the lawn at the corner of East Fulton St. and the crossroad just west of the Zant Landscape Home. It stands about fifty feet from the road, with a specimen of *C. punctata*, and is numbered 2 on a metal tag attached close to the trunk. Herbarium specimen 2. Pl. II, Figs. 10, 14; Pl. VI, Figs. 22 *a–c*; Figs. 8 *a–d*, 22.

Crataegus "burnt-orange"

A shrubby form 3–8 feet tall, spreading from several small trunks; of vigorous growth and stout twigs. Twigs dark purple to red-brown, with small outstanding lenticels; older twigs gray. Spines slender, few, 3 4 cm., straight, light brown, becoming gray with age. Outer bud scales coriaceous, glabrous, entire, light brown, yellow-brown to shining red-brown. Inner bud scales glabrous, entire, broad-ovate with rounded tip. Margins densely glandular with sessile, white and orange glistening resinous glands. Surface densely glandular with stipitate, white and orange glistening glands. Inner bud scales recurved as the bud opens; revolute on the margins; green and light red. Inflorescence 4 5-

flowered, opening as the leaves unfold. Bracts linear to slightly broad, persistent when the flowers open, with conspicuous glistening orange glands. Flower buds globose to broad and flat. Calyx light green, sometimes slightly bronze in young buds; glabrous. Calyx tube narrowly cylindric, of medium length, becoming abruptly turbinate. Calyx lobes foliaceous, red-tipped, narrowly triangular with deep broad sinuses, serrate and glandular with sessile to short-stipitate, glistening glands which become dull red, not yet reflexed when the flowers open. Tips of the calyx lobes in the young buds distinctly exceeding the size of the bud, meeting and twisting above the petals. Petals white; some flat, some cupped and full on the margins; spread of the petals 1.5–2 cm. Stamens 10, white, pollen present and plentiful. Styles 2–4. Leaves in the bud thin to thick, folded on the midrib, plicate, twisted and ruffled on the margins, frequently orange-tinted. Petioles glandular. At time of opening of the flowers the leaves are not yet entirely unfolded, and they recurve distinctly on the midribs. Stipules present, linear, lunate, some lobed and some with basal divisions, serrate with stipitate glands. Mature leaves 5–8 cm. long, ovate, the greater number ranging from 5 to 7 cm., distinctly but not deeply lobed, the two lower sinuses frequently distinctly obtuse; margins serrate to the acute tip and usually to the base, the serrations distinctly red-tipped; base slightly unequal in some; veins conspicuous below, surface glabrous above and below, subcoriaceous to coriaceous. Petioles distinctly glandular, red, grooved the entire length, slightly wing-margined. Stipules early deciduous. Summer color bright apple-green, whitish below; autumn color yellow. Mature leaves distinctly recurved on the midrib and dished. Autumn color green, merging to orange or dull orange, especially around edges of the leaf. Fruit 1.5–2 cm. long and broad, globoid and oblate, flat or only slightly conical at the pedicel end; with distinct angular hips near the pedicel end in many fruits. Pedicel 1.5–3 cm. long, glabrous. Calyx deciduous or usually persistent, as large as the fruit, red, with a distinct collar, tips of the lobes recurved. Margins of the lobes distinctly serrate. Fruit green or dull yellow, pubescence absent, bloom slight; flesh medium thin, green, hard. Nutlets

2–4, short (5–6 mm.), not all fertile, ridged and grooved on the back, ventral cavity absent. Frequent on flood plains and in rich pastures. A typical specimen may be seen in the hedgerow of the first crossroad running parallel to M–16 about a mile east of the Ridgemore Country Club. The plants are shrubby and scattered along the line of the old rail fence. Herbarium specimens 44, 72. Pl. I, Figs. 3 *a–b*; Pl. II, Fig. 13; Pl. VII, Figs. 23 *a–c*; Figs. 9 *a–d*, 23.

Crataegus "flabellate"

A shrubby form of irregular contour, rising 9 feet high. Spines slender, 3–4 cm. long, straight or slightly curved, dark brown, many. Outer bud scales glabrous, coriaceous. Inner bud scales membranaceous, glabrous, entire or the inmost serrate at the base, densely glandular on the margin with sessile or short-stipitate, dull red glands. Surfaces of the scales with few glands; position spreading; margins flat; scales deciduous after the leaves unfold; enlarging to 1 cm. in length, light brown and green. Stem growth long when the leaves unfold. Leaves in the bud glabrous or with a few long hairs, thick, medium green; position horizontal. Mature leaves 4–6 cm., mostly 4–5 cm. long, ovate, broad-ovate, orbicular, or many conspicuously flabellate, the flabellate forms broadest at about one half of the way up; margins with lobes shallow to medium, serrate and doubly serrate; bases mostly equal; truncate at the base or abruptly tapering or cuneate; tips rounded on the flabellate forms, abruptly acute on the others; sinuses acute; surfaces of the leaves glabrous above and below; subcoriaceous to coriaceous. Petioles sparingly or not at all glandular, grooved the entire length, slightly wing-margined on the vegetative shoots. Stipules early deciduous, linear, lunate, serrate, and glandular. Summer color above, olive-green to olive-yellow-green; lighter below. Position of leaves horizontal. Inflorescence about 10–flowered, usually slightly less. Bracts glandular, linear. Leaves opening before the flowers. Flower buds globose, green, glabrous. Calyx tube turbinate. Lobes narrow with broad sinuses, keeled; margins entire, tips slightly red-brown. Petals white, spreading 1–1.5 cm., cupped, mostly erect. Stamens

fewer than 10, often abortive, often none, white; some pollen present. Styles 3. Fruit 1–1.5 cm. long, 1–1.5 cm. wide, ovoid or cylindric and mostly conspicuously three-angled; bases flat or slightly conical; pedicels 0.5–2 cm. long, glabrous. Calyx persistent or not persistent, few as large as the fruit; erect or flat. A few show a conspicuous collar; most of them have none. Calyx lobes entire, narrow, glabrous. Fruit yellow to orange, green-mottled, sometimes vermilion; lenticels conspicuous, pubescence absent, bloom wanting; flesh thin, yellow-green, hard, acid. Nutlets 3, ridged and grooved on the back; ventral cavities absent. Shrubs infrequent in rich uplands. A typical specimen is located in Paris Township, Section 2, in the hedgerow above the truck-gardening farm south of Highway 116. Herbarium specimen 97. Pl. VII, Figs. 24 *a–c*; Figs. 10 *a–d*, 24.

Crataegus Crus-galli

A symmetrical tree, dome-shaped on top, usually slightly broader than tall. Outer branches angle upward or downward from near the trunk at about 5 feet from the ground. Height 10–20 feet; often several trunks form the contour of a single tree. Spines range from 4 to 8 cm., many, brown becoming gray, slightly recurved. Outer bud scales coriaceous, light brown to red-brown, pubescent, rounded on the tips, deciduous before the leaves unfold. Inner scales entire or a few lobed, moderately glandular on the margins with white or brown, clear or dull sessile glands; color green, white at the base; scales erect, enlarging to 1 cm. in length; stem growth short when the leaves unfold. Leaves in the bud erect, dark green, glabrous, thick. Outer bud scales wrapped, the inner folded on the midrib and plicate. Stipules early deciduous, linear, lobed, glandular, entire. Mature leaves 5–6 cm., a few 9 cm.; oblong-ovate to oval, often straight-sided, all longer than broad, the widest part at about three fourths of the distance up; some leaves with 1 or 2 irregular lobes; margins serrate and doubly serrate; bases cuneate, entire; tips acute, sometimes abruptly acute from the broadest part, giving a flat-topped appearance; sinuses acute, shallow; veins conspicuous above, inconspicuous below; surfaces above and below glabrous except

along the veins where there are brown woolly hairs; texture coriaceous. Petioles eglandular, slightly to entirely grooved, wing-margined, red at the enlarged base. Summer color above, dark green to olive-green, shining; below, light green to rusty yellow-green, dull. Contour of the leaves erect and horizontal. Inflorescence flat-topped, 10–20-flowered, blooming May 25 to June 5. Bracts linear, glandular, straw-colored, with red glands. Leaves before the flowers. Flower buds green, glabrous or with a few hairs on the pedicel, cylindric to globose. Calyx tube long, narrow, obconic. Lobes narrow with broad sinuses, descending, entire, eglandular or only occasionally with a few glands. Petals white, smooth or full, flat or cupped, spreading or reflexed. Throat of the calyx yellow inside. Stamens 10 or fewer, white or pale pink, some abortive and merging into petals, many shrunken. Styles 2. Fruit 1–2 cm. long, 1.5–2 cm. wide; angled; globoid, oblate, or cylindric; straight-sided; flat or slightly concave at the base. Pedicels 1–3 cm., glabrous, or with a few hairs. Calyx persistent, entire or with a few minute teeth, glabrous or with a few hairs, often as large as the fruit; flat or recurved, red. Collar absent or very slight. Color vermilion-scarlet to red-brown; lenticels conspicuous; pubescence wanting, bloom slight or wanting; flesh thick or thin, yellow or green, hard or mealy. Nutlets 2, without sinuses, ridged and grooved; ventral cavities absent. Variety "early" varies in being early. It is in full bloom by June 1. Variety "very early" differs in time of blooming. It is past bloom by June 1. Common on river flood plains, in upland pastures, and on hillsides. A typical specimen may be seen under the large elm on the flood plain of Plaster Creek just north of the schoolhouse at the intersection of Kalamazoo road and the side road leading to the country house. Herbarium specimen 1 A. Pl. VIII, Figs. 25 *a–c*; Figs. 11 *a–d*, 25.

Crataegus punctata

A tree growing 8–20 feet tall, narrow at the base but spreading abruptly at about 5 feet into a flat, open, conical head. Usually nearly as broad as tall, sometimes broader than tall, often with several small trunks making the contour of a single tree, often

with lower branches spreading and angling to the ground. Branches evident at a glance, not completely concealed by the leaves. Trunks very spiny. Twigs pubescent, light brown, dull, the year's growth becoming gray. Spines slender to medium, ranging from 4 to 6 cm., straight or slightly curved, with marked lenticels, dark mahogany-brown, red-brown, or light brown, usually light-tipped, few or many; old spines gray. Winter buds broad-ovoid, angular, 2–4 cm. long, cherry-red to brown; lower scales dull. Outer bud scales glabrous, ovate, or broad-ovate, keeled, acute, and apiculate, some rounded on the tip; entire. Inner scales membranaceous, pubescent, entire, sparsely glandular with small, sessile, red, white, or brown, dull or glistening glands; surface of the inner scales eglandular; position erect, margins flat. Scales deciduous before the leaves unfold, enlarging to 2 cm.; color light red, yellow-brown, yellow with red tip, or green with a light red tip. Stem growth short when the leaves unfold. Leaves in the bud densely pubescent, thick, the inner folded on the midrib and plicate, the outer wrapped; color medium green to yellow-green, grayish; position erect, becoming horizontal. Stipules early deciduous. Inflorescence about 10–20-flowered, mostly 10–18. Pedicels 1–1.5 cm. long. Bracts linear, glandular with stipitate, red glands. Flower buds globoid to ovoid, pale green, densely pubescent. Calyx tube narrow, obconic. Calyx lobes reflexed early, even in the bud; sinuses broad, lobes triangular, narrow, entire, keeled on the back, often red-tipped, hairy within (margins of the calyx lobes occasionally with a few serrations). Petals range from 1 to 2 cm., slightly cupped, margins smooth; position flat or strongly reflexed; color white. Stamens 10–20, mostly 20, dark red, purple-red, pink or white; full. Styles 2–4, mostly 2 and 3. Mature leaves range from 3 to 7 cm. long, mostly from 4 to 6 cm., a few ovate-oblong or oval, but mostly obovate; widest above the middle, some distinctly lobed from one third of the way up, many not lobed; margins serrate and doubly serrate; bases mostly symmetrical, cuneate, wing-margined to the base of the petiole, thus giving the appearance of a long, narrow leaf; sinuses acute; tips acute, many abruptly so; veins impressed above; surface sparsely pubescent above

and below; coriaceous or subcoriaceous. Petioles not glandular, slightly pubescent, grooved or not grooved. Stipules early deciduous. Summer color above, dark green or olive-yellow-green, dull; below, rusty yellow-green or light green. Autumn color dull yellow or falling without change. Fruit 1 2 cm. long, 1–2 cm. wide; ovoid, obovoid, or cylindric, but straight-sided, with a broad shoulder near the calyx, rounded on both ends and often somewhat angled; base concave, flat, or conical. Pedicel 1–2 cm. long, pubescent. Calyx persistent, not so large as the fruit; position flat or recurved. Collar absent or very slight; color red, becoming black. Lobes entire or infrequently with a few serrations, narrow, often acuminate, glabrous, or slightly pubescent; color red-brown, yellow, dark red, or dark red with purple tints; stamens persistent; lenticels conspicuous, pubescence absent or a few long hairs at the base, bloom wanting. Flesh thick, yellow or green, hard, acid. Nutlets 2 3, infrequently 4, distinctly ridged and grooved, some flat on the back; sinuses shallow or none; ventral cavities absent. Fruit usually abundant. Many trees along the river flood plains and in upland pastures. Common along roadsides and frequent in rich upland woods. Typical specimens may be seen in abundance along Plaster Creek east from Madison Avenue. Herbarium specimen 3. Pl. I, Fig. 4; Pl. VIII, Figs. 26 *a–c*; Figs. 12 *a–d*, 26.

Crataegus succulenta "nearly smooth"

A tree 10–12 feet tall, or a shrubby form. Spines range from 3 to 6 cm. long, straight or slightly curved, purple-red to dark brown, many. Outer bud scales light brown to red-brown, coriaceous; acute or rounded on the tips, fringed on the margins. Inner scales membranaceous, glabrous, entire or with few serrations at the base, moderately glandular on the margins with sessile or short-stipitate, clear or dull, white or red glands; surfaces eglandular. Inner scales enlarge to 1.5 cm. in length, erect or recurved; margins flat; color green with light red or pink. Stem growth long when the leaves unfold. Inflorescence about 10-flowered. Bracts glandular, linear. Leaves before the flowers. Flower buds globose, green, glabrous. Calyx tube short, broad,

obconic, and turbinate. Calyx lobes narrow, triangular, reflexed; serrate and glandular with short- or long-stipitate, red glands, sometimes red tipped with white; keeled. Petals spread 1–2 cm., mostly 1–1.5 cm., slightly cupped; position flat. Stamens 20, pink, full. Styles 2–5. Leaves in the bud glabrous or with a few hairs above at the angles of the veins; medium green and bronze; position erect. Stipules present, early deciduous, linear, some lobed or with basal division, serrate at the base, and stipitate-glandular. Mature leaves 4–8 cm. long, oblong-oval or broad-ovate, some approaching flabellate, longer than broad, mostly broadest at the middle, distinctly lobed above the middle; serrate; bases symmetrical, abruptly tapering, cuneate, or rounded; tips acute to rounded; sinuses shallow to medium, acute; veins conspicuous below; surfaces glabrous above and below, texture subcoriaceous. Petioles eglandular, 1.5–2 cm. long, red at the base, grooved on half the length and wing-margined. Summer color above, olive-yellow-green, shining; below, lighter; position horizontal. Fruit 0.75–1.5 cm. long, 1.5–1.7 cm. broad, globoid and oblate, flat at the base. Pedicels 1–2 cm. long, pubescent. Calyx persistent or deciduous, in some specimens as large as the fruit; position flat; collar present; color red. Calyx lobes serrate, broad, with acuminate tip; a few hairs persistent; stamens persistent. Color scarlet, lenticels conspicuous; surfaces glabrous; bloom wanting; flesh medium thick, hard to mealy, mild. Nutlets 2–5-ridged on the back; ventral cavities present. A typical specimen located in the pasture along Grand River flood plain on the river road north of North Park. One turns to the left at the first road before the one leading to the rifle range, then to the right on the road used by the cottagers and goes to the end. The specimen is in the pasture to the right, within a radius of one hundred yards of the corner of the pasture. Herbarium specimen 99. Pl. IX, Figs. 27 *a–c*; Figs. 13 *a–d*, 27.

Crataegus succulenta "big-bud"

A shrubby form 12–15 feet tall, spreading from many small branches; not contorted or twiggy; presenting a smooth appearance. Spines 3–7 cm. long, shining red-brown, curved gradually

from the point of attachment. Outer bud scales coriaceous, glabrous, very large, broad-ovate, rounded on the tips, red. Inner scales membranaceous, glabrous, serrate, sparsely to moderately glandular with short- or long-stipitate or sessile, dull red glands; surfaces occasionally with a few glands. Position of the inner scales spreading, finally recurving to the base of the bud, inner scales enlarging to more than 2 cm., light brown or green with light red midvein. Stem growth long when the leaves unfold. Young shoots horizontal with buds standing erect. Inflorescence 20–25-flowered. Pedicel about 1 cm. long, villose. Bracts linear, red-tipped, glandular. Leaves before the flowers. Flower buds green, sparsely villose. Calyx tube cylindric or obconic. Calyx lobes narrowly triangular with broad sinuses, serrate on the margin and glandular with stipitate, dull red glands; keeled. Calyx red in throat. Petals white, spread 1–1.5 cm., cupped; margins generally rough, position flat. Stamens 20, pink, full or infrequently shrunken. Styles 2–4. Leaves in the bud pubescent, folded on the midrib and plicate, bright green, erect. Stipules present, early deciduous, small, very narrowly linear, some lunate; red, glandular. Mature leaves enlarge to 7 cm. long, obovate, doubly serrate; veins impressed; surface above, villose to hispid, below, densely villose on either side of the veins. Petioles villose above, wing-margined the entire length, dark green, shining. Fruit size 0.5–1.5 cm. long, 0.5–1 cm. wide; ovoid, obovoid or less often pyriform; conical at the base. Pedicels 1–3 cm. long, pubescent. Calyx persistent, large as the fruit; collar present, color red. Calyx lobes serrate, hairy. Fruit scarlet to vermilion-scarlet; lenticels inconspicuous; pubescence present, bloom wanting; flesh thin, yellow, mealy. Nutlets 2, slightly ridged; ventral cavity present. A very neat form throughout the season, which would seemingly be of value in landscape design. The variety is found along the flood plains of Grand River and Plaster Creek as well as along minor streams in the vicinity. A typical specimen may be found along the bank of the stream to the left from the intersection of Madison Avenue and Plaster Creek. It stands close to the embankment and is sending out shoots along the bank where the soil is washing off. It is along the creek about

one-half mile east from the Madison Avenue bridge. Herbarium specimen 8 A. Pl. I, Fig. 5; Pl. IX, Figs. 28 *a–c*; Figs. 14 *a–d*, 28.

Crataegus succulenta "slow"

A shrubby form 6–12 feet tall, irregular in habit, found on river flood plains, and conspicuous for its late budding and late blooming. Spines 3–4 cm. long, slightly curved, dark brown becoming gray, few. Outer bud scales glabrous, broad-ovate, keeled, acute at the tip and apiculate, light brown. Inner scales membranaceous, glabrous or with a few hairs on the very inner ones, withering at the tips, finely fringed-serrate, sometimes lobed, sparsely to moderately glandular with sessile or short-stipitate, dull white glands; surfaces eglandular. Position of the inner scales erect or recurved; margins flat; scales enlarging to 2 cm. in length; color green and light red, white, or yellow-brown. Stem growth long when the leaves unfold. Inflorescence 10–25-flowered. Flowers bloom from June 1 to June 10. Pedicels 1–1.5 cm. long, bracts linear, glandular. Leaves appearing before the flowers. Flower buds ovoid to globose or cylindrical; green, densely pubescent. Calyx tube cylindric or obconic. Calyx lobes narrow, triangular, long, with broad sinuses, serrate and glandular with long-stipitate, dull red glands, keeled. Petals white, spread 1–1.5 cm., full and cupped; position spreading or flat, sometimes reflexed. Stamens 10 15, in some trees 20, white or pink, full or shrunken. Styles 2. Fruit 8 mm. to 1 cm. long, 7–9 mm. wide, obovoid or short-cylindric or sometimes globoid, flat at the base. Calyx persistent or deciduous, as large as the fruit, recurved and lying flat on the fruit. Pedicels 0.5–1 cm. long, stout, with a few hairs. Collar slight, lobes red with green tips, serrate with long teeth and often with persistent glands, narrow, hairy. Fruit mostly in pairs in the inflorescence; scarlet to vermilion-scarlet with conspicuous lenticels; a few short hairs on the surface; bloom slight or wanting; flesh thin, yellow, mealy, mild. Nutlets 2, slightly ridged and grooved, or rounded on the back; ventral cavities present. Some trees have many abortive fruits; others are well fruited. A frequent variety on flood plains of Plaster Creek and Grand River. Sometimes found in rich upland

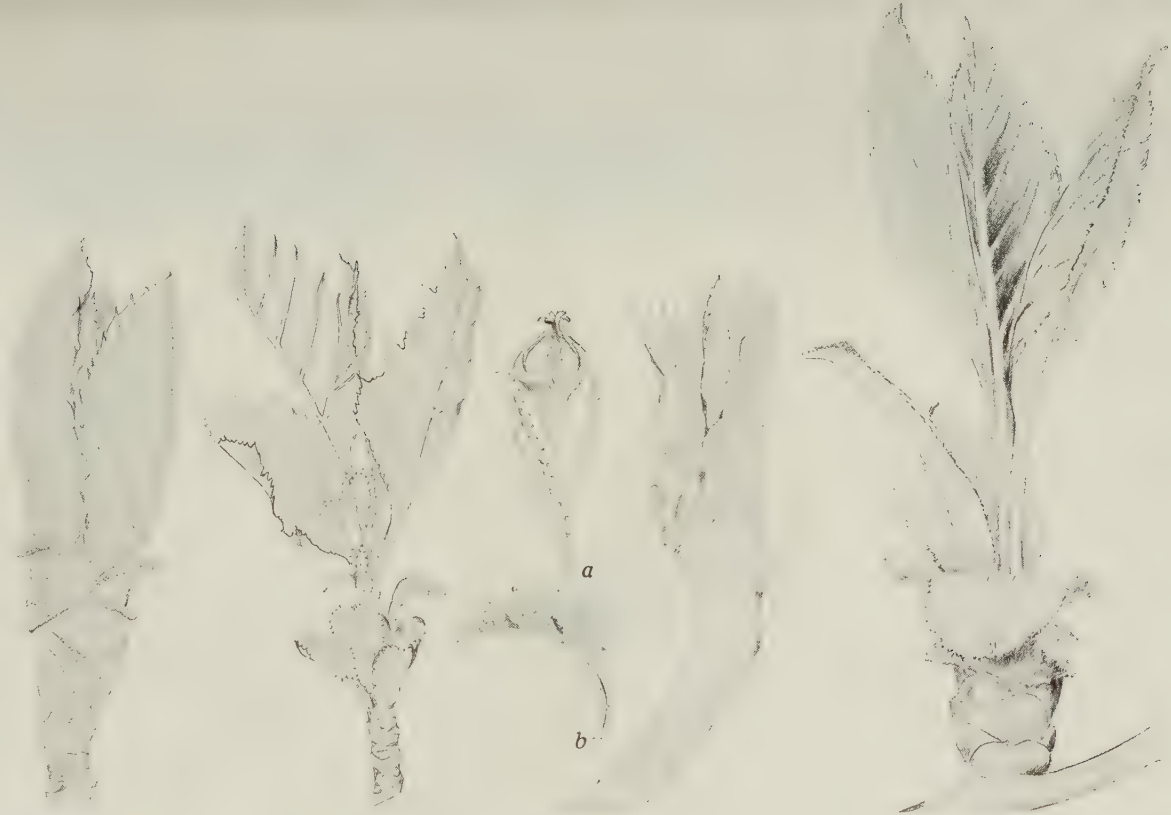
pastures. A typical specimen may be found about one-half mile back along Plaster Creek, east from Madison Avenue bridge. Several in a group stand about one hundred feet from the stream. Herbarium specimen 121. Fig. 29.

Crataegus succulenta "large-fruit"

A broad, rounded tree 12–15 feet tall, growing in upland pastures. Spines 3 4 cm. long, stout, distinctly curved; young spines light brown, older red-brown, dark-tipped. Lenticels inconspicuous, light, vertical, lens-shaped, few. Outer bud scales glabrous, broad-ovate, apiculate. Inner scales membranaceous, entire, densely glandular on the margins with short- or long-stipitate, brown glands. Surface of the inner scales with few glands. Position erect, enlarging with the developing stem to 2 cm., light brown to red-brown. Stem growth long when the leaves unfold. Inflorescence about 20-flowered. Bracts linear. Leaves before the flowers. Flower buds cylindrical, green, densely pubescent. Calyx lobes narrow, serrate, with dull red glands, keeled. Petals white, with spread 1.5–2 cm., cupped; position flat. Stamens 20, pink, shrunken. Styles 2. Leaves in the bud pubescent, folded on the midrib and plicate, dark green, horizontal in the opening bud. Stipules present, early deciduous, linear, glandular-entire. Mature leaves 4–9 cm. long, ovate, oval, or rounded; a few as broad as long; distinctly lobed above the middle, entire, 1 cm. at the base; serrate and doubly serrate, teeth brown-tipped; bases unequal, cuneate, tapering abruptly, or rounded. Tips abruptly acute; sinuses acute, shallow, veins conspicuous below; surface above, glabrous; below, densely pubescent with appressed hairs; texture subcoriaceous to coriaceous. Petioles eglandular, grooved the entire length, wing-margined. Summer color above, dark green, shining but less than in *Crataegus Crus-galli;* below, light green. Leaves form erect clusters on the new growth. Fruit size 0.75–1 cm. long, 1–1.5 cm. wide; many distinctly globoid and oblate; slightly angular, flat at the base. Pedicels pubescent, about 1 cm. long, but the secondary pedicels 3–4 cm.; clusters erect. Calyx persistent, larger than the fruit, flat. Collar slight. Calyx lobes long, pubescent, serrate the entire length, with per-

sistent glands. Styles frequently persistent and erect. Fruit pubescent, vermilion-scarlet; bloom wanting. Nutlets 2, ventral cavity present. This variety shows the largest fruit of any of the *succulenta* group. A typical specimen may be found in the hedgerow along the valley just north of the Perkins fruit farm on the crossroad between Knapp and East Leonard. Herbarium specimen 66.

Grand Rapids Junior College
Grand Rapids, Michigan



1. *C. mollis* 2. C. "bronze" 3 *a–b*. C. "burnt-orange" 4. *C. punctata* 5. *C. succulenta* "big-bud"

All figures are enlarged × 2

PLATE II

6. *C. mollis*

7. C. "bronze"

8. C. "red-calyx"

9. C. "dainty"

10. C. "right-angle"

11. C. "bronze"

12. C. "cut-leaf"

13. C. "burnt-orange"

14. C. "right-angle"

Flower bud and bracts (Figs. 6–10) and stipules (Figs. 11–14) of Crataegi. All figures are enlarged × 2

PLATE III

15. *C. mollis* 16. C. "bronze"

(*a*) Vegetative (or flowering) branches, (*b*) fruiting branches, and (*c*) mature fruits of Crataegi, arranged in the order in which the species bloom

PLATE IV

17. C. "cut-leaf" 18. C. "red-calyx"

(*a*) Vegetative (or flowering) branches, (*b*) fruiting branches, and (*c*) mature fruits of Crataegi, arranged in the order in which the species bloom

PLATE V

19. C. "claw-spine" 20. C. "woodcliffe"

(*a*) Vegetative (or flowering) branches, (*b*) fruiting branches, and (*c*) mature fruits of Crataegi, arranged in the order in which the species bloom

PLATE VI

21. C. "dainty" 22. C. "right-angle"

(*a*) Vegetative (or flowering) branches, (*b*) fruiting branches, and (*c*) mature fruits of Crataegi, arranged in the order in which the species bloom

23 C. "burnt-orange" 24. C. "flabellate"

(*a*) Vegetative (or flowering) branches, (*b*) fruiting branches, and (*c*) mature fruits of Crataegi, arranged in the order in which the species bloom

PLATE VIII

25. *C. Crus-galli* 26. *C. punctata*

(*a*) Vegetative (or flowering) branches, (*b*) fruiting branches, and (*c*) mature fruits of Crataegi, arranged in the order in which the species bloom

PLATE IX

27. *C. succulenta* "nearly smooth" 28. *C. succulenta* "big-bud"

(*a*) Vegetative (or flowering) branches, (*b*) fruiting branches, and (*c*) mature fruits of Crataegi, arranged in the order in which the species bloom

FOSSIL PLANTS FROM THE POCONO (OSWAYO) SANDSTONE OF PENNSYLVANIA

CHESTER A. ARNOLD

ALTHOUGH the occurrence of plant remains in the rocks below the coal horizons in Pennsylvania has been known for a long time, contributions to our knowledge of them have been few. The only comprehensive treatment of these plants is contained in the third volume of Lesquereux's *Coal Flora*, published in 1884 (3), in which are listed all the fossil plants of the United States below the Permian then known. About twenty species are given from the Pocono sandstone from five localities in Pennsylvania and West Virginia. Aside from casual references to plants in the Pocono in the later literature, practically nothing more has been done with them. This lack of attention is due largely to the massive character of the sandstone and to the fact that the Pocono is relatively unimportant economically. There are few large quarries in this formation; those which are opened are operated for but a short time, and the plant remains, if they are uncovered, rarely receive scientific attention.

Quite recently the present author was fortunate in securing five fossil plant specimens which had been collected by Mr. Paul Stone from a small quarry in the Pocono (Oswayo) sandstone about two miles northeast of Port Allegany, McKean County, Pennsylvania. The material had come into the possession of Mr. J. C. Galloway of Port Allegany, who, appreciating its possible scientific value, very generously submitted it for study.

The quarry in which the plants were found, known locally as the DeLong Quarry, is situated in a hillside about one hundred feet above the valley floor. Underlying the valley is the Catskill (Cattaraugus) formation. The Pocono, which rests on the Cats-

kill, commences somewhere between the quarry and the foot of the hill and extends to the top.

The lower ten or twelve feet of rock exposed in the quarry consists of hard massive sandstone cracked in various directions. Above this lies a bed, two feet or less thick, consisting of yellow mud and sand, with included fragments of charred wood, irregularly disposed. Some of the fragments are infiltrated with iron pyrites.

Though the Pocono has long been accepted as the basal member of the Mississippian in northern Pennsylvania, some recent stratigraphical studies have brought out evidence indicative of its Upper Devonian age (2). It is beyond the scope of this paper to deal with this subject at length, but the bearing of the plant remains upon it will be discussed.

THE PLANT REMAINS

The fossils consist of two impressions of fronds (*Archaeopterides*), an articulated leafy stem (*Articulatae*), a flattened strobilus (*Sigillaria*?), and a piece of pyritized wood (*Callixylon*).

One of the archeopterids is a portion from near the top of a sterile frond (Pl. X, Fig. 1). In most respects it agrees with *Archaeopteris Roemeriana* Goeppert forma *conferta*, as figured by Nathorst in his Plate 6, Figure 1 (4). The margins of the pinnules of our specimen are slightly toothed because of the outward projection of the individual veins. This feature is not apparent in Nathorst's figure and is not mentioned in the description, but such slight differences are often the result of preservation. Otherwise, the Pocono specimen conforms well with the description of this rather variable species.

Archaeopteris minor Lesq., which is claimed to bear some resemblance to both *A. Roemeriana* Goeppert and *A. hibernica* Forbes, is listed by Lesquereux (3, Vol. 3) from the Catskill and Pocono of Pennsylvania, but is inadequately figured and does not resemble our specimen as closely as do Nathorst's figures of *A. Roemeriana* Goeppert. All three of the species mentioned above are quite variable, and *A. hibernica* Forbes differs chiefly in having larger pinnules.

The other specimen from the DeLong Quarry, doubtfully referable to *Archaeopteris*, is the upper half of a single pinna closely resembling *Rhacopteris circularis* Walton (6), from the Teilia Beds (lower Carboniferous) of Flintshire, Wales. The main difference is in the veins of the pinnules, which are about twice as numerous in our form. The pinnules are circular in outline, symmetrical or nearly so, and contract at the base to form a short footstalk, which is set obliquely to the axis (Pl. X, Fig. 3). The entire specimen is fifteen centimeters long and tapers gradually to the apex (Fig. 30). The second and third pinnules at the lower left-hand corner of Figure 30 are shown enlarged in Plate X, Figure 3. Though this specimen bears some resemblance to *Rhacopteris*, it is often difficult, in the absence of fructifications, to distinguish between *Rhacopteris* and *Archaeopteris*.

Fig. 30. Specimen resembling *Rhacopteris sp.*, mentioned in text. Natural size

Another specimen of considerable interest and probably having lycopodiaceous affinities is a flattened, partially carbonized strobilus measuring approximately three by nine centimeters and tapering slightly from the base to the apex. The sporophylls, which stand out at right angles from the axis, are in verticils, and those in adjacent verticils alternate with each other. The strobilus is attached to a stout peduncle about six centimeters long. The verticillate arrangement of the sporophylls suggests affinities with the articulated stem described above, but the sporangia are more suggestive of a lycopod, possibly *Sigillaria*.

Most of the wood fragments in the mud bed above the sandstone were bituminized or charred beyond ready identification. A few pieces had undergone partial pyritization, so that the pitting is preserved and discernible along the radial surfaces, and one specimen, when examined by reflected light, shows the grouping of the pits characteristic of *Callixylon*. The preservation is too poor to permit the examination of any other anatomical features of the specimen, or specific identification.

The term "Articulatae" was designed to include those pteridophytes, both living and fossil, with jointed stems. The only living genus of this group is *Equisetum*, but in Paleozoic times it was represented by numerous forms such as *Calamites*, *Sphenophyllum*, *Pseudobornia*, and others.

One of the Pocono fossils of undetermined affinities, which, however, appears to belong to this group, is a portion of a jointed stem with whorls of linear leaves (Pl. X, Fig. 2). Although thin, the leaves appear to have been rigid, because instead of being appressed to the stem in the impression they stand out from it somewhat in their original position. Though this specimen shows certain features clearly enough to identify it as a member of the *Articulatae*, it is impossible to determine the nature of the plant or to refer it to any known genus. For convenience in reference it is placed tentatively in the genus *Trochophyllum*, which was founded by Lesquereux (3) for plants doubtfully referable to the *Calamariae*. Since this genus is indeterminate and may receive any form with whorled leaves, it is a convenient generic designation for our Pocono specimen.

Trochophyllum breviinternodium, sp. nov.

(Plate X, Fig. 2.)

Stem slightly less than one centimeter in diameter; nodes two millimeters apart. Leaves about fifteen millimeters long, two millimeters broad at the apex and narrowing gradually to point of attachment; about twenty per whorl.

Formation and locality. — Pocono (Oswayo) sandstone; Port Allegany, McKean County, Pennsylvania.

EVIDENCES CONCERNING THE AGE OF THE POCONO

Although this meager flora can be of but small use in establishing the age of the Pocono as Upper Devonian, it seems to support the suggestion (2). *Archaeopteris* is the most indicative fossil in this respect, although the flora as a whole has the aspect of being an old one. The specimen referred to *Trochophyllum* bears no close resemblances to any of the well-known *Articulatae* of the Carboniferous and is probably one of the primitive forms of the group. The discovery of a strobilus resembling *Sigillaria* is not surprising, because there are several lycopodiaceous forms from Devonian rocks. *Callixylon* is relatively common in the upper Devonian rocks above the Tully Limestone in New York and is predominantly a Devonian genus, although the black shales of Indiana and some of the neighboring states which have yielded large quantities of the wood and branch impressions of *Callixylon Newberryi* (Dn.) Elkins et Wieland are probably of Mississippian age (1).

Several species of *Rhacopteris* are characteristic of certain lower Carboniferous horizons of Europe, and the single doubtful *Rhacopteris* specimen in our collection would of course indicate an age no older than basal Mississippian for the Pocono if there were no other Devonian forms associated with it. But since there is some uncertainty concerning its generic identity, and since it occurs associated with *Archaeopteris*, the balance of evidence (so far as this meager flora permits one to judge) points to a Devonian age for the Pocono in this vicinity.

In Volume 3 of the *Coal Flora* (3) Lesquereux reports several species of *Archaeopteris* from the Pocono of Pennsylvania and West Virginia in association with forms which, if correctly identified, suggest an age later than Devonian. But he gives no Pocono localities in Pennsylvania north of Mauch Chunk, and since the range of many of the forms mentioned in his account is unknown, it is well to leave them out of consideration for the time being and to base our conclusions upon only the better-known forms. Neither is there any certainty whether the so-called "Pocono" of these more southern localities represents exactly the same facies as in

the localities farther north. He also mentions numerous finely preserved and large specimens of *Archaeopteris* in the Red Shale (which is probably Catskill, instead of Pocono, as he supposed) along the Susquehanna River above Pittston and Meshoppen.

Since the Pocono is situated in close proximity to the boundary between these two great systems of the Paleozoic, the plant remains are of considerable phylogenetic and stratigraphic interest. A more complete knowledge of the Pocono flora would probably show considerable overlapping of upper Devonian and lower Carboniferous types, a situation similar to that revealed by the Elberfeld flora of Germany, where the early and late Devonian floras, formerly supposed to be distinct, were found to meet and overlap (5). Such a condition is indicated by the association of forms resembling *Archaeopteris* and *Rhacopteris* in the Pocono.

University of Michigan

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FIG. 1. *Archeopteris cf. Roemeriana* Goeppert resembling forma *conferta* Nathorst. × 1

FIG. 2. *Trochophyllum breviinternodium*, sp. nov. × 1

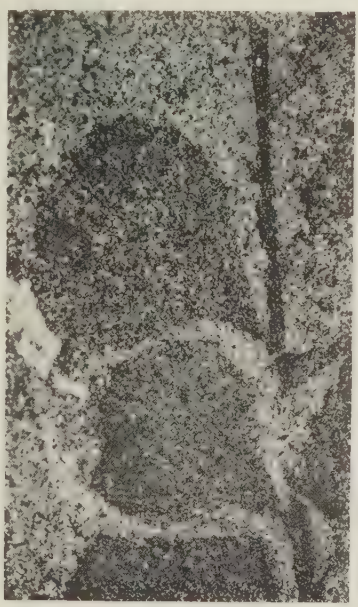


FIG. 3. Pinnules of *Rhacopteris* (?) *sp.* Enlarged to show detail. × about $2\frac{1}{2}$. Compare text figure 30

All specimens are from the Pocono sandstone, Port Allegany, Pennsylvania

AN ECOLOGICAL STUDY OF BRYANT'S BOG, CHEBOYGAN COUNTY, MICHIGAN*

HELEN COBURN, DORIS DEAN, AND GERTRUDE M. GRANT

GENERAL DESCRIPTION AND HISTORY

BRYANT'S BOG is a small kettle-hole bog near Douglas Lake in Cheboygan County, Michigan. Notwithstanding its small area it is one of the deepest bogs of the region and presents a very interesting problem from any of several angles.

The bog, which is almost circular in outline, 107 by 115 meters, was 3.2 feet above Douglas Lake in 1926. At the center is a crescent-shaped lake, pH 5, surrounded by a Chamaedaphne mat. On the east side the mat extends to the upland without a well-defined high-shrub line; on the west side there is a definite high-bush thicket. The upland surrounding the bog was originally a beech-maple forest, in which there were a few very large pines, but, since the lumbering and burning of the area, *Populus tremuloides* and *Betula papyrifera* form the dominant tree growth.

When the bog came under the observation of the Biological Station of the University of Michigan in 1909 it was for the most part a typical Chamaedaphne association. The unusually dry year of 1921, characterized by low water everywhere in the vicinity, marked a change in the appearance of the bog. Before 1921 in all but the southern and western parts no Nemopanthus was seen above the Chamaedaphne, but in the following year the bushes of Nemopanthus could be seen scattered over the outer portion of the bog and beginning to top the Chamaedaphne. By 1925 it could be termed a Chamaedaphne-Nemopanthus consocies, and is now rapidly passing from this stage to a Nemopanthus association (see Pl. XI, Figs. 1–2).

* Contribution from the Biological Station of the University of Michigan. The work at Bryant's Bog was done under the direction of Professor F. C. Gates during the summers of 1927 and 1931.

Within the history of the Biological Station *Carex lasiocarpa* has advanced out into the lake at a few places. By rapid invasion Chamaedaphne overtook the Carex, limiting it to a narrow zone. The lake is now surrounded almost completely by Chamaedaphne, which is attempting to invade the water itself, but is making slow progress.

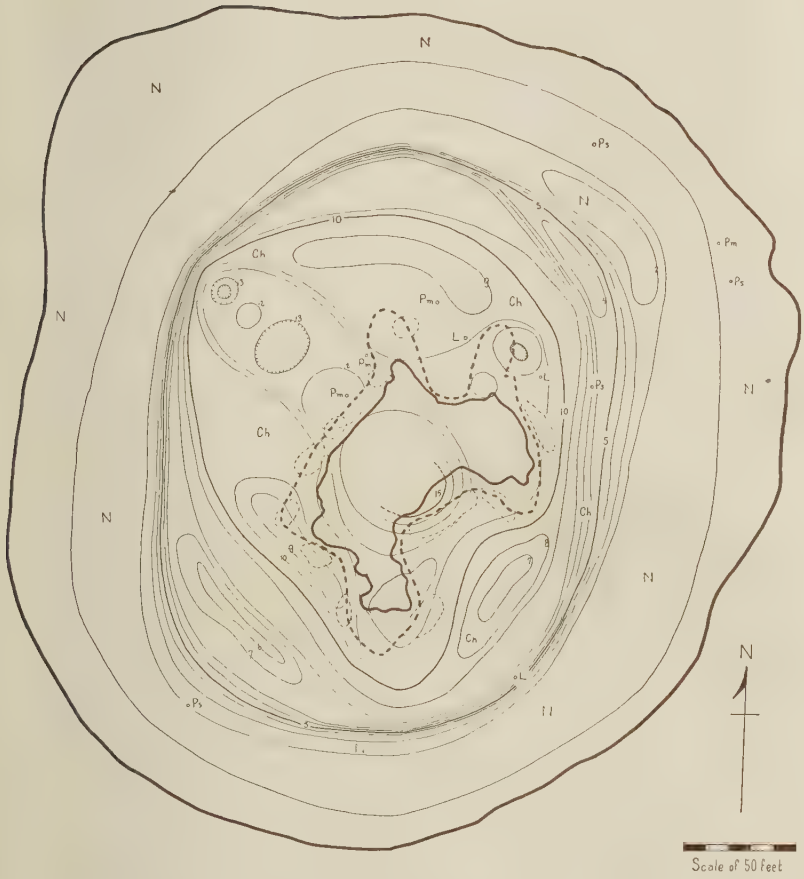
Open water at one time extended to the outer margin of the bog, but the development of the mat has decreased the size of the lake to 30 by 41 meters, and even within the history of the Biological Station the area of the lake has noticeably diminished (see Map 1).

Ultimate extinction of the lake has been delayed by conditions which have limited life in the water. In the early history of the lake there was probably oxygen in the water to a great depth. Then followed a reduction in the dissolved oxygen of the water as the process of filling in proceeded. This reduction, together with the humic acids and noxious gases formed from partial decay of plant remains, is responsible for the limited fauna.

In 1911 there was oxygen in the surface water, but practically none below it. Now conditions are reversed, and although the amount of oxygen is still small, it is greater at a depth of two feet than at the surface.

The rather rapid rise of the false bottom in the last few years has been indirectly the cause for the slight increase in oxygen content. In 1912 there were fifteen feet of clear water above the false bottom, and in that year the depth as recorded by a six-pound sounding lead was thirty feet. In 1918 the false bottom had risen to within seven and one-half feet of the surface and the lower depth recorded was eighteen feet. There were two feet of clear water above the false bottom in 1919; this condition has prevailed with but little variation since.

Although the false bottom offers but slight resistance to any weights lowered, there is sufficient consistency to furnish anchorage for such bog water plants as *Scirpus subterminalis* and *Utricularia intermedia*. The former uniformly although not densely covers the false bottom; the latter is near and under the Chamaedaphne at the edge of the lake.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A few plants of *Nymphaea advena* are well established in the bays of the lake, and although numbers of small plants can be seen below the surface, the interference of collectors using dip nets has checked their more rapid advance and increase.

The Chamaedaphne overhanging the margin of the lake is rapidly invading the water, and with the continued rise and filling in of the false bottom the lake in time will entirely disappear.

Shoreward for several feet from the lake the mat is quaking, a feature most pronounced near the bays. The easiest approach to the bog is from the northeast side, which explains the convergence of paths at the head of the northeast bay. The absence of Chamaedaphne here is due to the continued walking and tramping of people. This might break down the present growth of Sphagnum sufficiently to cause the lake to enlarge at this point.

MAT ASSOCIATIONS

Two associations predominate on the mat, *Chamaedaphne calyculata* and *Nemopanthus mucronata*. The Chamaedaphne, however, owing to invasion by Nemopanthus and trees, is no longer a pure association. In the Chamaedaphne association twenty-five contiguous quadrats, each one meter square, were taken on four lines. A frequency index of these one hundred quadrats showed *Vaccinium oxycoccus* (73 per cent), *Kalmia polifolia* (48 per cent), and *Andromeda glaucophylla* (46 per cent) to be the most numerous species growing with the Chamaedaphne and Sphagnum.

FREQUENCY INDICES OF PLANTS OF CHAMAEDAPHNE MAT

Chamaedaphne calyculata	99	Vaccinium canadense	23
Sphagnum spp.	98	Smilicina trifolia	14
Vaccinium oxycoccus	73	Nemopanthus mucronata	11
Carex trisperma	50	Larix laricina	10
Kalmia angustifolia	48	Eriophorum virginicum	10
Andromeda glaucophylla	46	Betula papyrifera	6
Moss	37	Aronia arbutifolia	5
Picea mariana	35	Vaccinium pennsylvanicum nigrum	4
Gaylussacia baccata	35	Vaccinium pennsylvanicum	4
Sarracenia purpurea	31		

Menyanthes trifolia	4	Habenaria obtusata	1
Drosera rotundifolia	2	Habenaria blephariglottis	1
Pinus strobus	2	Melampyrum lineare	1
Utricularia intermedia	2	Trientalis americana	1
Acer rubrum	1	Quercus borealis	1

With the exception of a few small areas Chamaedaphne is abundant and in a healthy condition. During 1915 Sphagnum to be used for packing was removed from an area of several square meters from the northwest corner of the lake. At the same time Chamaedaphne with which the Sphagnum had been growing was pulled up and tossed aside. *Eriophorum viridicarinatum* and *Eriophorum virginicum* invaded the depression left by the removal of these plants, but Chamaedaphne is beginning to reclaim this territory, and the first indications of returning Sphagnum were noticed in 1927. By 1931 it was hardly possible to outline the patches with certainty. *Vaccinium canadense* has practically crowded out the Chamaedaphne from a considerable area in the southeast part of the bog.

The *Nemopanthus mucronata* association forms a definite high-shrub thicket on the south and west sides of the bog from southeast to northwest. On these sides the shrubs have a uniform height of about two meters and are advancing in a solid line, except in the northwest part, where the fringe is irregular. Here large clumps of Nemopanthus of the same height as those of the fringe close off an area of Chamaedaphne.

There is an absence of a high-shrub line from north to southeast, where Nemopanthus is more scattered over the Chamaedaphne mat, invading as individual plants which have not yet formed clumps. Although Nemopanthus plants ranging in height from one to one and one-half meters are overtopping the Chamaedaphne, the shrubs are not so high as those of the thicket (Pl. XI, Fig. 2).

Aronia arbutifolia, which is sparingly present with the Nemopanthus, was found only where the Nemopanthus does not form the thicket. *Ilex verticellata*, usually found in Nemopanthus associations, was absent from the bog mat, but a few individual shrubs were seen in the fosse. There is an abundance of *Gaylussacia*

baccata and *Vaccinium nigrum* in both Nemopanthus and Chamaedaphne associations of the northeast and east sides of the bog, where the bog merges gradually with the upland.

Large trees ranging in height from four to nine meters are scattered irregularly over the mat and form a broken fringe near the lake margin, but those of *Picea mariana* are merely slender snags or scraggly trees such as one usually finds in such a habitat. Further detrimental factors are the dwarf mistletoe, *Razoumofskya pusilla*, which has produced characteristic witches'-brooms on the Picea (Pl. XI, Fig. 1), and the sawfly larvae, which have caused the death of the Larix trees.

By far the most numerous seedlings and young trees on the mat are *Picea mariana*, which in the south and southwest parts of the bog are especially abundant and extend almost to the margin of the lake. *Pinus strobus* and *Larix laricina* are less numerous than Picea, though they are more uniformly distributed on the mat. Young Larix trees have not yet shown evidence of injury from sawfly larvae, and both seedlings and older trees of *Pinus strobus* have an especially vigorous appearance.

In the Nemopanthus thicket, overtopping and advancing beyond its edge, are a number of *Betula papyrifera* trees. These are sparingly present on other parts of the mat, but prefer the shelter of the high shrubs. The open aspect of the bog to the northeast and east accounts for the few seedlings of *Populus tremuloides* on the mat of that area. Only a few seedlings of *Acer rubrum* are on it, and these are in the southeast part, where there are a few larger trees of the species near the bog margin and in the fosse. Single seedlings of *Pinus resinosa* and *Quercus borealis* were observed on the northwest line. Both these species are in the upland near the bog and may in time become more numerous on the mat. *Tsuga canadensis* and *Abies balsamea* are likewise represented on the mat by a very few trees. No *Thuja occidentalis* seedlings have been found, though seeds have been scattered at the northeast end. Thuja grows along the shore of Douglas Lake not far from the bog and might be expected in the bog at the present time.

FOSSE

There is apparently a distinct relation between the character of the fosse and the nature of the high-shrub thicket. From north to southeast, where Chamaedaphne extends with the Nemopanthus to the bog margin, the fosse alternately widens to two or three meters and narrows so that it is practically extinct. Chamaedaphne and Nemopanthus entirely fill it in a few places, even encroaching on the aspen upland. In several places *Gaultheria procumbens* has spread across the fosse into the bog area. Where the fosse is distinct in this section it is open, dry, and moss-covered, or filled with Vaccinium and *Galussacia baccata*. Chamaedaphne surrounds an area of *Scirpus atrocinctus* two to three meters wide and five to six meters long near the north end. Fallen logs are characteristic of all the fosse area, but are not numerous in this eastern part.

Behind the high-bush thicket the fosse widens, but instead of being open, as on the east side, there is a dense growth of plants in greater variety. Ferns, tree seedlings, Nemopanthus shrubs, and characteristic fosse plants with fallen logs and brush produce a tangled mass that distinctly separates the bog mat from the upland. Nemopanthus shrubs have completely closed in several small sections of the fosse.

There is no longer standing water in the fosse; except at the beginning of the summer season or after heavy rainfall it is almost dry.

Evidences of fire occur on logs and stumps in or near the fosse area, especially at the east, south, and west parts of the bog, and at the bases of the taller trees on the bog mat. One snag 24 cm. in diameter had been burned on the south side several feet above the base. There has been no fire, however, within the history of the station.

DEPTH DETERMINATIONS

To determine the depth of Bryant's Bog peat readings were taken at intervals of 3.05 meters on eight lines from the edge of the lake to the outer margin of the bog. For this survey a regula-

tion Davis peat borer was used. From the figures thus obtained depth contours of one-meter intervals have been sketched on the map. These show a decided cliff formation on the north, northwest, and west lines, repeated more or less opposite on the southeast line. The other lines show more gradual slopes, with several islands interspersed, indicating a terracing of the slope.

The peat near the lake was in a more or less liquid state for some meters down and offered little — in some places no — resistance to the borer. In the immediate vicinity of the lake and for some distance back it was necessary to hold the borer in position while adding lengths, to keep it from slipping out of sight.

On all lines sand was encountered after a certain number of meters, but not solid ground. With but little effort the borer was forced down through several layers of varying thickness evidently composed of sand.

A slight rumbling and bubbling noise could be heard when pockets of gas were struck as the borer was pushed through soft peat, whether near the lake or several meters from its edge. Most of the gas was methane, and bubbles coming to the surface could be ignited. In a few places the gas escaped with such violence as to send pieces of soft peat several decimeters above the mat.

Solid, well-preserved logs were encountered on each line at varying depths from close to the surface to two meters below the mat. They were most abundant on the entire east line and on the half of the southwest from the margin toward the lake.

Samples of peat varied much in color and texture, and microscopical examination showed pine pollen to be present at all depths.[1] Samples of sand varied from a coarse light yellow material with or without white or bluish pebbles to a smooth pinkish substance evidently mixed with clay. No samples of blue clay and no pure clay without sand were taken.

[1] A study of pollens with relation to depth in this bog was made in 1931 by Potzger, J. E., "Succession of Forests as Indicated by Fossil Pollen from a Northern Michigan Bog," *Science*, 75 : 366. 1932.

PLATE XI

Photograph by G. M. Grant

FIG. 1. View of Bryant's Bog looking northeast, showing general aspect of the bog, with the witches'-brooms of the Picea evident

Photograph by G. M. Grant

FIG. 2. View of the bog looking west, showing invading clumps of Nemopanthus in the foreground

SUMMARY

1. Bryant's Bog is a small deep peat bog, 107 by 115 meters, near Douglas Lake in Cheboygan County, Michigan.

2. The present vegetation consists largely of the Nemopanthus association, fully developed on the west and south sides, and, since 1921, replacing the Chamaedaphne association on the east and north sides. Scattered throughout the bog, especially near the lake, are trees, many of which are diseased. If the seedlings of these trees continue to develop, the bog will become tree-covered.

3. The fosse was formerly well developed, but in several places it is now disappearing on account of the filling in of plants.

4. Peat of all gradations was taken, from liquid to solid, some with well-preserved plant structures, some wholly disintegrated.

5. Samples below the peat are of two types: coarse, gritty sand and fine sand mixed with clay.

6. Pollen grains of Picea and Pinus were present at all depths, Larix not below five meters, and Acer, Fagus, and Alnus nearer the surface.

University of Michigan Biological Station
Cheboygan, Michigan

OBSERVATIONS ON THE DISTRIBUTION AND FLOWERING OF CERTAIN LEMNACEAE IN MICHIGAN

LLOYD C. COCHRAN AND RAY NELSON

THE occurrence of flowers of *Lemna minor* L. and the wide distribution of lemnaceous plants in Michigan during the summer of 1931 are of considerable interest to plant ecologists. Such seasonal development is unusual and correlates well with the abnormal weather during the summer.

Flowers of *Lemna minor* (Pl. XII, Fig. 1) were first noted in drainage ditches in the celery marshes at Kalamazoo, Michigan. Upon examination the water was found to be very stagnant. At harvest time the celery growers dispose of the celery trimmings by allowing them to decay in drainage ditches. The Lemna was most abundant in a central pool into which the ditches drained. The plants formed a dense mat over the entire surface of the pool, and the flowers could easily be seen without the aid of a hand lens.

Similarly, *Lemna minor* was found in blossom in the Grand River at Lansing, Michigan. The plants were most abundant near sewage outlets and downstream from them; their number dwindled in proportion to dilution of the sewage. Flowers occurred only near the point of entrance of the sewage. These facts again show the close affiliation of the flowering habits of Lemna with stagnation and large amounts of organic matter in the water. Flowers of Lemna also grew in the celery marshes at Muskegon, Michigan; in the college lily pool at East Lansing, Michigan; and were forced in stagnant water in the greenhouse. In water cultures with distilled water and salts the flowers failed to develop.

The first evidence of flowers in *Lemna minor* is the formation of a small hump near the edge of the thallus. Upon examination under the low power of the microscope the four pollen sacs may

be clearly seen, appearing as almost sessile spherical bodies imbedded in the thallus. These soon push out and grow up from the edge of the thallus by elongation of the filament. Contrary to Marie-Victorin,[1] there may be either one or two stamens on each plant. Only a few pistils were found, and these appeared to be immature or aborted. Beal, in *Michigan Flora*,[2] says that *Lemna minor* is very common in Michigan and sometimes flowers in June. The observations described in this paper were made in the latter part of August and the first part of September. Inquiry by the authors revealed that the flowers of *Lemna minor* are very rare in Michigan and possibly have never been seen; Beal took his statement from literature which applied to forms farther south.

Other lemnaceous plants growing with *Lemna minor* are *L. trisulca*, *Spirodela polyrhiza*, *Wolfia columbiana* (Pl. XII, Fig. 2), and *W. punctata*. None of these was in flower, although the vegetative forms were much more abundant than in previous seasons. The two species of Lemna and the Spirodela are common in the vicinity of Lansing, but the wolfias have not been reported from Ingham county. All grew in close association, and were most abundant near sewage drains, but were common in stagnant water in various locations.

It is the opinion of the writers that this seasonal growth and the flowering of these plants is dependent upon several ecological factors. Since such plants flourish in stagnant places, a very important requirement is a suitable medium. The deficiency in the amount of rainfall and the excess of high temperatures during the summer of 1931 greatly lowered streams, lakes, and ponds, and increased stagnation of water in general. Such a condition may possibly account in no small measure for the unusual occurrence of these forms.

Michigan State College
East Lansing, Michigan

[1] Marie-Victorin, Frère, "Les Spadiciflores du Quebec," *Contrib. Lab. bot. de l'Univ. de Montreal*, No. 19: 1–60, 27 figs. 1931.

[2] Beal, W. J., *Michigan Flora: A List of the Fern and Seed Plants Growing without Cultivation*, Reprinted from the *Fifth Annual Report of the Michigan Academy of Science*, Vol. 5. 1904.

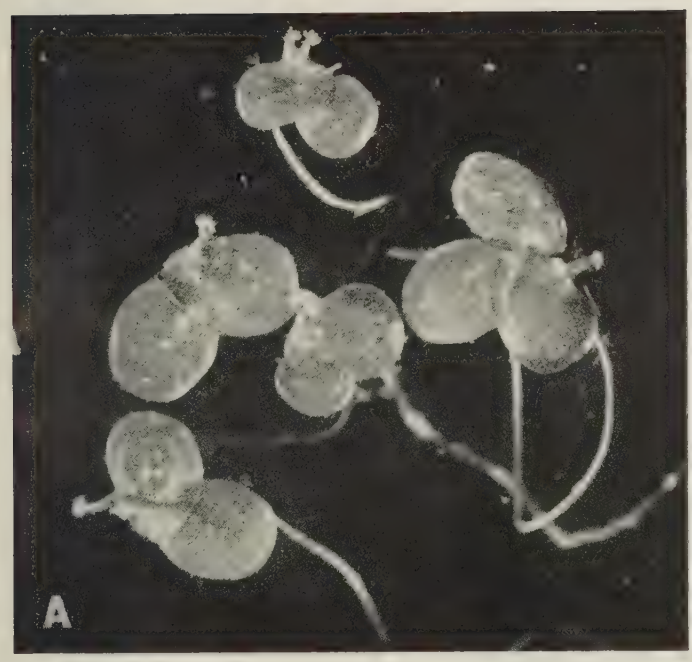


FIG. 1. Photomicrograph of *Lemna minor* plants with stamens growing from the edges of the thalli. × 8

FIG. 2. Photomicrograph of vegetative thalli of *Wolfia columbiana*. × 25

SOME REPRESENTATIVE SPECIES OF BAZZANIA FROM SUMATRA *

ALEXANDER W. EVANS

IN 1927 Professor H. H. Bartlett made a small but interesting collection of Hepaticae in Sumatra. It contains several species of Bazzania, or "Mastigobryum," as it is often called, a genus typified by the well-known northern species, *B. trilobata* (L.) S. F. Gray, but attaining its highest development in the Indo-Malayan region. The present paper is based on Professor Bartlett's material, but includes one species from a later collection.

Most of the species of Bazzania are large and conspicuous and are distinguished from other leafy Hepaticae by their prostrate or ascending shoots, with more or less imbricated incubous leaves, the apices of which are usually dentate. The shoots branch in one plane, apparently by successive dichotomies, and are attached to the substratum by means of slender flagelliform branches with reduced, scalelike leaves. These branches arise in the axils of underleaves and grow directly downward. The genus is uniformly dioicous, and the short and highly specialized sexual branches also take their origin in the axils of underleaves. These are much smaller than the lateral leaves and also differ from them in form and method of attachment to the stem. Other generic characters are enumerated in taxonomic works on the Hepaticae.

In a preliminary synopsis of the genus, under the name Mastigobryum, Stephani divided it into eleven sections; [1] and Schiffner, a few years later, recognized the same sections under the generic name Bazzania.[2] In 1908 and 1909 Stephani published his monograph of the genus Mastigobryum and raised the following four

* Contribution from the Osborn Botanical Laboratory.

[1] *Hedwigia*, 25: 244. 1886.

[2] In Engler und Prantl, *Die natürlichen Pflanzenfamilien*, 1[3]: 101. 1893.

of his earlier sections to subgeneric rank: Integrifolia, Bidentata, Tridentata, and Inaequilatera.[3] The species discussed below include one representative of the Integrifolia and nine of the Tridentata, the latter being made up of seven sections, which correspond for the most part with sections of the preliminary synopsis. Stephani's subgeneric and sectional names, with feminine endings, are adopted in the present paper.

SUBGENUS INTEGRIFOLIAE

Bazzania loricata (R. Bl. & N.) Trevis.

Jungermannia loricata R. Bl. & N. Nova Acta Acad. Leop.-Carol., 12: 233. 1824.
Mastigobryum loricatum Nees in G. L. & N., Syn. Hepat., p. 217. 1845.

Plate XIII

Summit of Dělěng Baroes, Karoland, June 21, 1927, H. H. Bartlett 8489a. This interesting species was based on specimens collected in the mountains of Java and has since been reported from the Philippines, Malacca, and Sumatra. No. 8489a agrees with a specimen in the Mitten Herbarium, which is presumably a part of the type material. The general features of the species are clearly shown by Lindenberg and Gottsche's figures.[4]

The plants of *B. loricata* grow in depressed mats, often mixed with other bryophytes, and show a rich, golden-brown color, becoming darker and duller in the older parts. The robust shoots frequently attain a length of 6 cm. or more, but the living portions scarcely exceed 3 cm. The stems reveal a slight dorsiventral compression and usually measure 0.35 0.4 mm. in width by 0.25–0.3 mm. in thickness. The differentiation of the tissues into cortex and medulla is not strongly marked. A cross-section (Fig. 1) shows that the stem is composed of thick-walled cells, averaging throughout about 25 μ in diameter. All the walls are more or less pigmented with yellowish brown, those toward the periphery being somewhat darker than the others. The peripheral walls are

[3] *Bull. Herb. Boissier II*, 8: 683. 1908.
[4] *Spec. Hepat. Mastigobryum*, Pl. 4, Figs. 1–5. 1851.

further distinguished by their greater thickness. In the section shown the outermost walls are about 8 μ thick, whereas those toward the center are only 4–5 μ thick. Except for these slight differences in the color and thickness of their walls the cortical and medullary cells present much the same appearance. A longitudinal section (Fig. 2), however, reveals that the cortical cells, which are mostly 50–100 μ long, tend to be shorter than the medullary cells, which are mostly 100-200 μ long. The section also shows that all the cells are more or less definitely arranged in longitudinal rows; that the end walls tend to be thin throughout, especially when they approach a transverse position; and that the pits in the longitudinal walls are relatively infrequent. These pits can be distinguished in cross-sections also (Fig. 1).

The leaves, which are closely imbricate and distinctly convex, spread at a wide angle and are broadly ovate, gradually narrowing to a broad, rounded-to-truncate apex. In the present material the leaves are mostly 1.5–1.8 mm. long, 1.4–1.6 mm. wide at the base, and about 0.6 mm. wide at the apex. The dorsal base is rounded and arches across the stem; the ventral base is more variable, in some specimens being merely rounded and in others developing a minute inflexed auricle. The whole margin, except close to the base on each side, is serrulate, with the teeth tending to be longest in the apical region and gradually diminishing in length toward the base. In the apical region (Fig. 3) nearly every marginal cell projects as a tooth, but since the teeth vary considerably in length and extend in different directions a marked irregularity results. The outer wall of a normal tooth is strongly thickened, and sometimes the projecting portion consists almost entirely of thickened wall. Teeth of this type, however, are associated on young leaves with teeth in which the outer wall is less thickened (Fig. 3 *a*) or even thin throughout (Figs. 3 *b–c*). As the leaves become older these thin-walled teeth disintegrate more or less completely, thus increasing the irregular appearance. Backward from the apical region the teeth (Fig. 4) are more scattered and, perhaps in the majority of cases, consist entirely of thickened cell walls. Before their final disappearance the projecting portions become reduced to low crenulations. Although

the basal portions of the leaves are normally entire, some of them develop one or more irregular sinuations (Fig. 5) or blunt tooth-like projections (Fig. 6), associated with the evanescent slime papillae. In rare cases there is a persistent pit between a slime papilla and the adjoining cell, but usually the separating wall becomes strongly thickened, as in the examples figured.

The so-called "vitta," which forms a distinctive feature in leaves of various tropical species of Bazzania, is not clearly defined in *B. loricata*. It consists of a group of cells near the base of the leaf, which are distinguished from their neighbors by their arrangement in more or less definite longitudinal rows (Fig. 7) as well as by their elongate form. The transition between these elongate cells and the more isodiametric cells occupying most of the leaf area is sometimes gradual and sometimes fairly abrupt, as shown by Figure 8. The cells of the vitta average about 45 by 28 μ, whereas the isodiametric cells average about 28 μ in diameter. The marginal cells tend to be longer than broad, averaging about 25 by 13 μ, and their long axes form a wide angle with the leaf margin. Local thickenings of the walls (Figs. 3 8) are everywhere conspicuous and are normally in the form of trigones with convex or truncate sides. Many trigones are separated by well-marked pits, but coalescence of trigones is a frequent phenomenon and gives rise to quadrate or elongate thickenings. In some specimens the pits connecting a cell with its neighbors become obliterated by subsequent deposits of thickening. This process may take place in any part of a leaf, but is most pronounced in the marginal regions. Attention may be called also to the thick walls bounding the leaf cells both dorsally and ventrally. The surface of these walls, representing the leaf cuticle, is smooth, or nearly so, throughout.

The imbricated underleaves, which are free from the side leaves, are somewhat concave from below and are attached by a transverse or slightly oblique line. This curves downward a little at each end, where it meets the line of insertion of a side leaf. The underleaves are reniform in outline and usually measure 0.5–0.6 mm. in length and 0.8–1.2 mm. in width. The apex is broadly rounded, and the base is gently rounded on each side, occasionally

showing a vaguely cordate condition. Except at the very base the underleaves are bounded by a hyaline border, two to four (or rarely five) cells in width at the apex (Fig. 9) and thinning out to a width of a single cell on the sides (Fig. 10). The cells of this border are thin-walled, and the walls show very faint and irregular striations (not given in the figures), which apparently represent delicate fissures. The hyaline cells are irregular in form and some of them project slightly as vague crenulations. The transition between these cells and the thick-walled interior cells of the underleaf, which are essentially like the leaf cells, is usually abrupt, although an occasional cell at the junction may have a slight thickening of the wall. As the underleaves become older, the border disintegrates more or less completely and leaves a ragged edge.

The flagelliform branches, which reveal no signs of dorsiventrality, present few features of interest. Their cylindrical axes are mostly 0.15–0.18 mm. in diameter, and their thick-walled cells are much like those of the stem, except that the thickenings are less pronounced. The scattered scalelike leaves are suborbicular and measure 0.2–0.25 mm. in length. They are convex and more or less appressed to the axis, their apices are broad and truncate, their margins vary from subentire to irregularly crenulate or denticulate, and the thickenings in the walls of their cells are much like those of the leaf cells.

The original specimens of *B. loricata* were sterile, but the present material includes both male and female plants. Most of the male branches are 1–2 mm. long and apparently never proliferate. The closely imbricated, monandrous bracts, which are in four to six pairs, are in the form of compressed sacs (Figs. 11–12), ovate in outline, and composed of two subequal parts, connected by a rounded and strongly arched keel. The bracts are mostly 0.5–0.6 mm. long and each of the component parts is 0.3–0.45 mm. wide. The apex of the bract, which in many instances is involute (Fig. 11), is irregularly denticulate, but there are no distinct apical lobes. The bracteoles are convex and ovate, measuring about 0.45 mm. in length and 0.35 mm. in width; their apices are broad and truncate, and their margins show minute denticulations.

The perichaetial leaves are mostly in three or four series, and the bracts and bracteoles are essentially alike. They increase rapidly in size, upward, those of the basal or outermost series being only about 0.3 mm. in length, whereas those of the innermost series measure about 1.8 mm. in length and 1.5 mm. in width. These innermost leaves are broadly ovate, with rounded to subtruncate apices, and their margins above the middle are minutely and irregularly crenulate or denticulate. In the apical region (Fig. 13), where the denticulation is most pronounced, an occasional tooth may be in the form of a cilium, one or even two cells long. In most cases some of the submarginal cells bulge outward in the form of short, blunt or sharp, projections, two of which are illustrated (Figs. 13 *a*-*b*), and this process may take place on either surface of the leaf. The marginal teeth of the perichaetial leaves and the bulging, submarginal cells are shown in one of Stephani's unpublished figures, drawn from a specimen collected by Kurz on Mt. Salak, Java.

The perianths, which are lanceolate in outline, are about 0.9 mm. in diameter and many of them attain a length of 7 mm. Throughout the greater part of their extent they are perfectly terete, showing no signs of keels, but toward the apex they become plicate. Unfortunately, the perianths in the Sumatra material are old and badly weathered, so that the number and arrangement of the folds and the features of the mouth cannot be determined. Except in the upper part, where the cells are in a single layer, the perianth is fleshy and composed of two or three layers of cells. A cross-section at about the middle (Fig. 14) indicates that the outer cell walls are strongly thickened and form continuous membranes on both surfaces. In the interior the thickening is less pronounced and more irregular. In the unistratose portion of the perianth (Fig. 15) the structure is more delicate, since the outer walls are much thinner.

In addition to the thickenings just described the cells of the perianth often develop curious wartlike thickenings. These are occasionally found on the outside (Fig. 14 *a*), but much more frequently project into the cell cavities. Thickenings of this type are exceedingly variable in number and in form, as illustrated by

a surface view of a group of cells (Fig. 16), but hemispherical and short rodlike types predominate. It is not unusual for them to occur in pairs, one projecting inward from the outer wall of a cell and the other outward from the inner wall. This relation is given in Figure 15 *a*. Although these peculiar structures are most numerous in the cells of the perianth, they also occur in the cells of the perigonial and perichaetial leaves and may occasionally be detected in the cells of ordinary leaves (Figs. 5 *a–b*).

The species of the Integrifoliae are in need of careful revision, and some of the statements about them in the literature are ambiguous. In the case of *B. loricata*, for example, the descriptions of the underleaves do not state definitely whether a hyaline border is present or not. Lindenberg and Gottsche [5] describe the margins as entire, crenulate, or obsoletely denticulate, and it is apparent that this statement might apply to primary crenulations or denticulations or to the irregular projections left behind after a hyaline border had disintegrated. Stephani [6] states that the margin is denticulate, as in the leaves, and this might perhaps be interpreted to mean that a hyaline border is not present, since the leaves are destitute of such a border. His statement, however, is not definite on this point, and yet the idea that he did include under *B. loricata* specimens having underleaves without borders is supported by a figure in his unpublished Icones and by a specimen which he determined as *B. loricata*. The figure represents a detached underleaf and shows minute but definite denticulations in the apical portion. The source of the specimen from which the figure was drawn is not indicated. The specimen referred to *B. loricata* has distinctly denticulate underleaves, with no indication of a hyaline border. It was collected in 1906 by E. D. Merrill on the island of Mindoro in the Philippines (No. 5635). In the writer's opinion plants of this character should not be included under *B. loricata*, but only those in which the underleaves are distinctly bordered. Otherwise, too wide a range of specific variation would have to be assumed. The specimen from which Stephani made his drawing and the speci-

[5] *Spec. Hepat. Mastigobryum*, p. 13. 1851.
[6] *Bull. Herb. Boissier II*, 8 : 695. 1908.

men from Mindoro should, therefore, be referred to some other species.

Apparently, the only species of the Integrifoliae with which Stephani associates bordered underleaves is *Mastigobryum Semperi* of the Philippines.[7] The writer has not seen the original material of this species, but has examined in the herbarium of the New York Botanical Garden a specimen which Stephani referred to *M. Semperi*. This specimen, which agrees with his description and unpublished figures, may be considered authentic. It was collected by C. B. Robinson (No. 6595) on Mt. Banajao in the Laguna Province of Luzon, the island where Semper found the type. The relationship between *B. loricata* and *Mastigobryum Semperi* is very close, but the latter is the more robust; the leaves are about 3 mm. long, 2 mm. wide at the base, and 0.75 mm. wide at the apex. The leaves of *M. Semperi* are serrulate, much as in *B. loricata*, and show a few evanescent thin-walled teeth at the apex, but they tend to be a little shorter. The apex is further distinguished by being vaguely tridentate, a feature shown in Stephani's unpublished figure of a detached leaf. The hyaline border of the underleaves is even better developed than in *B. loricata* and is often five or six cells wide at the apex and three or four cells wide far down the sides. As a rule, the transition between the hyaline cells and the ordinary thick-walled cells of the underleaf is more gradual than in *B. loricata*. Although the differences between the two species are slight and largely quantitative, *M. Semperi* evidently represents a distinct species.

Another Indo-Malayan species which is very similar to *B. loricata* is *B. insignis* (De Not.) Trevis.,[8] originally described from specimens collected by O. Beccari in Sarawak, Borneo, but since reported from Amboina and the Philippines. De Notaris recognized the close relationship between the two, but pointed out certain differences in the leaves and underleaves. In *B. insignis*, according to his account, the leaves are obliquely cordate-attenuate-linguiform, with sharply serrulate margins, and the under-

[7] *Bull. Herb. Boissier II*, 8: 746. 1908.

[8] *Mem. Ist. Lomb.*, 13: 414. 1877. *Mastigobryum insigne* De Not. *Mem. Accad. Torino, Cl. Sci. Fis. Mat. II*, 28: 290; Pl. 18. 1874.

leaves are semicircular to subovate. In *B. loricata*, on the other hand, the leaves are said to be broadly deltoid-cordate, with shorter teeth, whereas the underleaves are described as reniform. The margins of the underleaves are said to be repand-crenulate, but this does not tell us whether hyaline borders are present or not. Stephani, however, is more definite. He describes the underleaves [9] as "integra minute serrulata," and one of his unpublished figures drawn from Beccari's material shows an underleaf entire below and minutely toothed above; the teeth agree with those illustrated in a figure of a detached leaf. It seems justifiable, therefore, to assume that the underleaves of *B. insignis* lack hyaline borders and thus differ in an important respect from those of *B. loricata*.

Other differences between the species are indicated by De Notaris in his description and figures of the perichaetial leaves of *B. insignis*. Those of the innermost series are shown to be attenuate-lanceolate from a narrow base, sharply serrulate in the upper part and two-, three-, or four-dentate at the narrowed apex. In *B. loricata* the apices of the innermost perichaetial leaves are rounded or subtruncate, and the margins are less conspicuously toothed.

SUBGENUS TRIDENTATAE

SECTION PARVISTIPULAE

Bazzania tridens (R. Bl. & N.) Trevis.

Jungermannia tridens R. Bl. & N. Nova Acta Acad. Leop.-Carol., 12 : 228. 1824.
Pleuroschisma tridens Dumort. Recueil d'Obs. sur les Jung., p. 20. 1835.
Mastigobryum tridens Nees in G. L. & N., Syn. Hepat., p. 227. 1845.
Bazzania tridens Trevis. Mem. Ist. Lomb., 13 : 414. 1877.

Plate XIV, Figures 1–11

Near triangulation pillar "D" on Dělěng Koetoe (near Kampong Goersinga), Karo Plateau, June 23, 1927, H. H. Bartlett 8536b. This common and widely distributed species was based on sterile material collected by Blume in Java. When Nees von Esenbeck redescribed it in 1830 [10] he commented on its great

[9] *Bull. Herb. Boissier II*, 8 : 746. 1908. [10] *Hepat. Javan.*, p. 60. 1830.

frequency on the island and distinguished two varieties, α and β. Variety β was soon raised to specific rank, under the name *Mastigobryum pectinatum*, by Lindenberg and Gottsche,[11] who restricted the specific name *tridens* to variety α. The species is still understood in this restricted sense. It was apparently known to the earlier writers from Java only, but has since been reported from Banca, Borneo, Celebes, Ceram, India, Japan, and Sumatra. Lindenberg and Gottsche give an excellent idea of the general aspect of the species.[12]

In the present material the plants grew in loose, depressed mats, in admixture with *B. paradoxa* and other bryophytes. They are brownish green; the younger parts are paler and more distinctly green. The living portions of the shoots measure 2–3 cm. in length, and the infrequent dichotomies are mostly 1–1.5 cm. apart, with widely divergent branches. The stems are about 0.35 mm. wide and 0.25 mm. thick, thus indicating a slight dorsiventral compression. A cross-section shows that the cell walls are pigmented with a pale brown; the color becomes deeper toward the periphery. The outermost walls (Fig. 1) are mostly 6 10 μ thick, but those in the interior are mostly 4–6 μ thick; sometimes, however, they are only 2 μ thick. Pits are abundant, but not always distinct, owing to the fact that the wall around a pit may thicken gradually rather than abruptly. Except for the differences in the thickness of the walls and in their pigmentation, the cortical and medullary cells are much alike. The cortical cells are about 22 μ in tangential width and 16 μ in radial width, whereas the more nearly isodiametric medullary cells average about 24 μ in diameter.

The leaves are loosely imbricate and widely divaricate, many of them forming an angle of 90 degrees or more with the stem. Although slightly convex when seen from above, they are scarcely, if at all, deflexed and lie approximately in a single plane. On well-developed plants the leaves are distinctly falcate and measure 1.2–1.5 mm. in length by 0.5 0.7 mm. in width. Their outline is more or less linguiform, with the dorsal and ventral margins

[11] *Spec. Hepat. Mastigobryum*, p. 84. 1851.
[12] *Op. cit.*, p. 81; Pl. 14, Figs. 1–5.

parallel throughout the greater part of their extent. At the dorsal base the margin is slightly rounded and arches to about the middle of the stem, but scarcely beyond. At the ventral base the margin is slightly rounded or straight, meeting the stem at an acute angle. The truncate apex (Figs. 2–4) usually bears three sharp, subequal teeth, separated by acute to obtuse sinuses and as a rule tipped with a row of two or three cells (Fig. 7). The teeth, however, are subject to variation in size and in number. The median tooth, for example, may be larger than the others, only two teeth may be present, or a fourth tooth may be developed, either on the side of one of the principal teeth or on the leaf margin below the other teeth. Aside from the apical teeth the margin is entire throughout.

The leaves have a fairly well defined vitta extending from the base to about the middle. It is separated from the margin on the ventral side by two or three rows of smaller cells and on the dorsal side by fifteen to twenty rows of still smaller cells. The transition between the vitta and the adjoining cells is less abrupt on the dorsal side than on the ventral. The cells of the vitta (Fig. 5), which is usually eight to ten cells broad in the basal part, are more or less elongate and show the usual arrangement in longitudinal rows. In their typical development they are mostly 30–40 μ in length and average about 20 μ in width. Their trigones, which rarely coalesce, are separated by broad pits and are relatively small, with slightly convex, straight, or slightly concave sides. Along the ventral margin (Fig. 6) the cells are mostly 12–15 μ long and 10–12 μ wide, whereas along the dorsal margin they average about 12 by 9 μ, with the long axes in both cases at right angles to the margin. The cells between the vitta and the dorsal marginal cells average about 14 μ in diameter; those in the apical part of the leaf (Fig. 7) are a little larger, averaging about 20 by 16 μ. Except in the immediate vicinity of the vitta the cell walls are slightly but uniformly thickened, without evident pits, or else they have small and indistinct trigones.

The underleaves (Figs. 8–10) are approximate to loosely imbricate, plane or nearly so, and closely appressed to the stem, which they slightly exceed in width. They are quadrate to quad-

rate-orbicular and usually measure 0.55–0.65 mm. in length and width. The line of insertion is transverse, but it curves or bends downward abruptly at one end, making the underleaf shortly decurrent. At the straight end the line meets the line of insertion of a side leaf, although there is no actual coalescence; at the curved end the line is separated by a short distance from the line of insertion of a side leaf. The underleaves are broad and truncate at the apex, and the margin may be slightly and vaguely sinuate or sparingly and irregularly dentate or sinuate-dentate; the teeth vary from acute to rounded. Marginal slime papillae are produced in considerable abundance (Fig. 11) and are sometimes long-persistent. Except at the very base the cells of the underleaves are thin-walled and hyaline. In a narrow basal area, however, one to three cells high, the cells are more or less chlorophyllose with slightly but uniformly thickened walls. The transition between this area and the hyaline tissue is gradual.

The flagelliform branches are about 0.15 mm. in diameter. Their scattered scalelike leaves are suborbicular, measuring about 0.25 mm. in length when well developed, and their margins are entire or nearly so. The leaves resemble ordinary underleaves in being almost wholly composed of thin-walled hyaline cells.

The Sumatra material of *B. tridens* is completely sterile, and the published descriptions tell us nothing about the male inflorescence and very little about the female. According to Lindenberg and Gottsche, the female branch arises either from the main stem or from a flagelliform branch, and the perianth, which projects far beyond the perichaetial leaves, is contracted and four-plicate in the apical part and denticulate at the mouth. This is apparently the extent of our information. Even Stephani, in his recent monograph of the genus, says nothing about the sexual branches, and the figures in his unpublished Icones show only the vegetative organs.

In Stephani's preliminary synopsis of the genus Mastigobryum he placed *M. tridens* and two other Asiatic species in a special group of his section Grandistipula, distinguished by underleaves which are but little wider than the stem. In his monograph he transferred all three species to his section Parvistipula, where they

more logically belong. The other two species in question are *M. assamicum* Steph.[13] of the province of Assam in northern India and *M. himalayanum* Mitt. of the neighboring province of Sikkim.[14]

Stephani's published figures of *M. assamicum*, which agree in most respects with the figures in his unpublished Icones, give a clear idea of the species, and his descriptions supply a number of additional details. The apical foliar teeth are much like those of *B. tridens*, as are the leaf cells and the underleaves. The leaves, however, are scarcely if at all falcate, and some of the underleaves were originally described as being connate with a side leaf. This latter feature is more clearly indicated in his published figures than in his Icones, where most of the underleaves shown are evidently free from the side leaves. In his later revised description, moreover, he makes no allusion to connate underleaves.[15] On the whole, the differences brought out between *M. assamicum* and *B. tridens* are very slight, and the species may prove to be synonymous.

Mitten's *M. himalayanum* seems to be more remote. Although the leaves of this species are falcate, much as in *B. tridens*, and although the apical teeth and the leaf cells have much in common, *M. himalayanum* may at once be distinguished by its reflexed underleaves, which are distinctly denticulate or dentate in the upper part. The features of the species are well brought out by Stephani's full description,[16] and also by the figures in his Icones.

Bazzania pectinata (Lindenb. & Gottsche) Schiffn.

Mastigobryum pectinatum Lindenb. & Gottsche. Spec. Hepat. Mastigobryum, 84; Pl. 14 (under *M. tridens*), Figs. 6–10. 1851.
Bazzania pectinata Schiffn. Nova Acta Acad. Leop.-Carol., 60: 259. 1893.

Plate XIV, Figures 12–19

Near triangulation pillar "D" on Dělěng Koetoe (near Kampong Goersinga), Karo Plateau, June 23, 1927, H. H. Bartlett 8545.

[13] *Hedwigia*, 24: 215; Pl. 1, Fig. 2. 1885.
[14] *Journ. Linn. Soc. Bot.*, 5: 105. 1861.
[15] *Bull. Herb. Boissier II*, 8: 756. 1908.
[16] *Op. cit.*, p. 760.

The original material of *B. pectinata* was collected by Blume in Java, but the species has since been reported from Amboina, Banca, Borneo, and Luzon. Lindenberg and Gottsche listed it from French Guiana also, on the basis of specimens collected by Meissner. This record has not been confirmed by later writers and is probably erroneous. The Sumatra specimens listed above are not in complete agreement with a Javan specimen in the Mitten Herbarium, which is presumably authentic, but the differences between them are hardly enough to warrant a specific separation.

The plants in the Sumatra material, which grew with other bryophytes in thin, depressed mats, are dull green, turning brownish with age. The shoots are mostly 1.5–2 cm. long, if the living parts only are taken into consideration, and the branches of the successive dichotomies are widely divergent. The stems are slightly compressed and most of them are 0.2–0.25 mm. in width by 0.18 0.2 mm. in thickness. A cross-section shows that one or two layers of cells on the outside may have pale brownish walls, but that the walls of the interior cells are unpigmented. Except for this slight difference the cortical and medullary tissues (Fig. 12) are much alike, and the average diameter of the cells is about 22 μ throughout the entire section. The cell walls are mostly 3–5 μ thick. The thickening is uniform (except for the pits), and the outermost walls are scarcely thicker than some of the interior walls.

The leaves are approximate to loosely imbricate and spread widely from the stem, with the angle often equaling or exceeding 90 degrees. They are slightly convex, when seen from above, but are not deflexed and tend to lie in a single plane. On well-developed plants the leaves are distinctly falcate, both dorsal and ventral margins being curved and forming subparallel lines. The leaves vary from ovate-linguiform to linguiform and usually measure 1.2–1.5 mm. in length by 0.4–0.55 mm. in width. The margin, at the dorsal base, is straight or very slightly rounded and extends scarcely beyond the middle of the stem; on the ventral side it meets the stem at an acute angle and is neither rounded nor auriculate. In the outer part the leaves narrow very slightly,

and the broad apex, which is rounded to truncate, is variable with respect to its teeth. In the more typical conditions (Figs. 13–14) these are definitely three in number and are in the form of broad and subequal triangles with subacute to subobtuse apices. Leaves of this type, however, are associated with those (Figs. 15–16) in which the teeth are irregular, indistinct, or variable in number, one, two, or even four being present. Occasionally, in fact, the teeth may be lacking altogether. In the Javanese specimens examined by the writer the plants are less variable, and leaves with three subequal teeth predominate. The leaves of *B. pectinata* have a strong tendency to break across in the basal portion and thus become detached. Such leaves represent *Bruchblätter* and play an important part in the vegetative reproduction of the species. They have been observed in several other species of Bazzania.

The vitta forms a fairly definite band of cells extending from the base to the vicinity of the apex. It is separated from the ventral margin by two to four rows of cells and from the dorsal margin by fifteen to twenty rows. In the basal part the transition from the vitta to the normal leaf tissue is fairly abrupt (Fig. 17), but is more gradual elsewhere. The cells of the vitta are mostly 25–40 μ long by 20–30 μ wide and are distinguished from the other leaf cells not only by their greater size but also by their more conspicuous trigones with convex or truncate sides. The trigones occasionally coalesce, but are usually distinct and separated by broad pits. Except in and near the vitta the cells (Fig. 18) have their walls slightly but uniformly thickened and thus show neither pits nor distinct trigones. They average about 11 μ in width along the margin and about 14 μ in diameter in the other parts of the leaf.

The underleaves are distant and small, measuring only 0.18–0.22 mm. in length and 0.22–0.3 mm. in width. They are broadly orbicular in outline, slightly convex from below, and closely appressed to the stem. The line of attachment is transverse throughout the greater part of its extent. At one end it almost meets the line of attachment of a side leaf, which stands at about the same level as the underleaf; on the other side, however, where

the side leaf is at a lower level, the line of attachment of the underleaf bends abruptly downward, thus causing a very short decurrence. The underleaves are rounded to subtruncate at the apex and entire along the whole margin, except for slight irregularities associated with the presence of slime papillae (Fig. 19). The cells of the underleaves soon lose their chlorophyll and are essentially the same throughout; the walls become slightly and uniformly thickened.

The flagelliform branches of *B. pectinata* are mostly 0.1–0.13 mm. in diameter, and their scattered scalelike leaves, except for their smaller size, are much like the underleaves on ordinary vegetative branches. In rare cases a ventral branch, instead of becoming flagelliform, develops into an ordinary leafy branch; and in still rarer cases a leafy branch becomes flagelliform in character.

The male inflorescence of *B. pectinata* is still unknown. Nees von Esenbeck, however, in his comments on "*Jungermannia tridens* β," gives a brief account of the perichaetial leaves, stating that they are numerous, densely circumvolute, small, delicate, and multifid. Other writers make no mention of the female inflorescence, with the exception of Schiffner, who notes that the perianth is bluntly three-keeled in the upper part and shortly laciniate at the mouth, and that the perichaetial leaves are toothed. The specimens from Sumatra are completely sterile.

Although *B. pectinata* was originally included under *B. tridens*, it is usually not difficult to distinguish one from the other. In *B. pectinata* the leaves are narrower than in *B. tridens*, the trigones in the cells of the vitta tend to be better developed, and the underleaves are smaller, more nearly entire, and their cells have firmer walls.

Another closely allied species is *B. densa* (Sande Lac.) Schiffn.,[17] originally described from Javan material collected by Teysmann, but since recorded from Malacca, Samoa, and Sumatra. This species, however, may be at once recognized by its reflexed underleaves.

[17] *Conspect. Hepat. Archipel. Indici*, 151. 1898. *Mastigobryum densum* Sande Lac., *Nederl. Kruidk. Arch.*, 3 : 418. 1854.

Bazzania fuscescens, sp. nov.

Laxe caespitosa, fusca, in partibus iunioribus pallidior; caules ascendentes, parce ramosi, ramis oblique divaricatis; folia contigua vel parum imbricata, oblique patula, ovata, 0.6 0.8 mm. longa, 0.35-0.5 mm. lata, apice tridentato dentibus triangulatis acutis, margine integro; cellulae tenerae, trigonis parvis; foliola remota vel contigua, subquadrata vel subrectangulata, apice truncato, parce et irregulariter dentato; flores ignoti.

Plants in loose mats, varying in color from dark lustrous brown to pale brown; stems (apparently) ascending, mostly 1–2 cm. long, sparingly branched, the living portion of an individual stem rarely showing more than one dichotomy; branches obliquely spreading; leaves approximate to loosely imbricate, slightly convex but not deflexed, spreading at an angle of about 60 degrees, somewhat falcate, ovate, mostly 0.6–0.8 mm. long (when well developed) and 0.35–0.5 mm. wide, truncate at the apex and usually sharply and subequally tridentate with shallow rounded sinuses, otherwise entire; leaf cells with small but usually distinct trigones, the vitta broad but vaguely defined, extending from the base to beyond the middle; underleaves distant to approximate, slightly convex (from below) and appressed to the stem, subquadrate to subrectangular, the width in the latter case slightly exceeding the length, mostly 0.2 0.3 mm. long and 0.25 0.35 mm. wide, sparingly and irregularly toothed, especially in the truncate apical portion, composed of cells with thickened walls usually showing trigones; inflorescence unknown.

Plate XV, Figures 1–15

Summit of Dĕlĕng Si Naboen (ascent from Kampong Goeroe Kinajan), Karoland, June 25–26, 1927, H. H. Bartlett 8639. Type in the herbarium of Yale University.

The material shows a slight admixture with a sterile Lepidozia, but is otherwise in pure condition. The slender stems, in their best development, are mostly 0.27 0.3 mm. wide and 0.2–0.24 mm. thick. In more delicate plants, however, the stems are considerably narrower and may be only 0.15 mm. wide. There are,

in fact, all gradations between normal leafy stems and flagelliform branches. Some of the ventral branches, moreover, are leafy from the beginning and some of the leafy branches become flagelliform as their growth continues.

The cells of the stem, as seen in cross-section (Fig. 1), show a slight contrast between cortex and medulla, although the transition from one to the other is gradual. The cells of the outermost, or cortical, layer are subquadrate and average about 25 μ in tangential and radial width; the interior, or medullary, cells average about 21 μ in diameter. The cell walls are pigmented with yellowish brown, the shade becoming darker toward the periphery. The outermost walls are mostly 8–10 μ thick, whereas the walls in the interior of the stem are only 2–4 μ thick. Pits are difficult to demonstrate.

In the normal position of the leaves the falcate character is scarcely noticeable, but shows more distinctly in leaves dissected off and spread out flat. The margin at the dorsal base is curved, but not rounded, and at the ventral base is straight or nearly so. Although the apical teeth are typically subequal (Figs. 2–3), they sometimes show variations in size, but there is nothing definite about the relative position of the larger tooth or teeth (Fig. 4). In poorly developed plants the teeth may be irregular or rudimentary, and their number may be reduced to two (Fig. 5).

The vitta, which is not clearly defined, occupies more than half the leaf area and extends well into the apical portion. Along the ventral side of the leaf, where it is most distinctly marked off, it is separated from the margin by one or two rows of cells; along the dorsal side, where it merges more gradually into the adjoining tissue, it is separated from the margin by eight to ten rows. The vitta itself is mostly ten to twelve cells wide at the base. Its cells (Fig. 6) are arranged in more or less distinct longitudinal rows, though they are relatively shorter than in most species of Bazzania; the widest cells are in general 25–30 μ wide and only 30–40 μ long. The trigones are distinct, with straight or slightly convex sides, and coalescences are very infrequent. The cells along the ventral margin (Fig. 7) are subquadrate and measure about 16 μ in width; those along the dorsal margin (Fig. 8)

are more variable in form and measure about 13 μ in width; those in the apical portion (Fig. 9) average about 20 μ in diameter. Except along the dorsal margin, where the cell walls are uniformly thickened, the cells show more or less distinct trigones, somewhat smaller than those in the vitta.

The sides of the underleaves (Figs. 10–14), which are subparallel or slightly convergent toward the base, are subentire or vaguely unidentate. The teeth at the truncate apex are in general two to six in number; they vary from rounded to subacute and are separated by shallow and usually subacute sinuses. All the marginal irregularities seem to be associated with slime papillae, vestiges of which are often apparent at the apices of the teeth or in the sinuses between them. The underleaves are destitute of hyaline borders, and their cells (Fig. 15) are essentially like the leaf cells, having slightly thickened walls and more or less distinct trigones. The line of attachment is straight or nearly so and may end at some little distance from the lines of attachment of the corresponding side leaves. More frequently, however, one end meets the line of attachment of a side leaf, and there may be a narrow, vague connation between them. Even when the ends are separated there may still be evidence of connation on one side, with the under leaf in consequence shortly and indistinctly decurrent.

The flagelliform branches, in their most typical development, are about 0.15 mm. in diameter, and their scattered scale leaves are mostly subquadrate and measure 0.12–0.15 mm. in length and width; in some cases, however, they are slightly longer than broad. The scale leaves are much like the underleaves in texture, and their apices usually show two or three irregular denticulations.

There is a certain resemblance between *B. fuscescens* and the more slender forms of the circumpolar *B. tricrenata* (Wahlenb.) Trevis., although Stephani, in his monograph, places the latter species in the Grandistipulae.[18] In the typical forms of *B. tricrenata*, however, the plants are more robust, the leaves are subcordate at the base and strongly deflexed, and the teeth or

[18] *Bull. Herb. Boissier II*, 8: 851. 1908. Stephani describes the species under the name *Mastigobryum triangulare* (Schleich.) Steph.

lobes of the underleaves are separated by deeper sinuses. The leaf cells afford additional differential characters, although the trigones are much alike. In *B. tricrenata*, for example, the contrast in size between the marginal and interior cells is less marked than in *B. fuscescens*, and the transition from one to the other is even more gradual. The basal and median cells, furthermore, tend to be more nearly isodiametric and show many deviations from an arrangement in longitudinal rows. It would be straining a point, therefore, to distinguish a vitta in the leaves, and no such structure is mentioned in the published descriptions of the species. In *B. fuscescens*, on the contrary, a vitta is evident, although less well marked than in many other species of the genus.

It may be recalled that Sande Lacoste once reported *B. tricrenata* from the Indo-Malayan region, under the name *Mastigobryum deflexum*.[19] His record was based on specimens collected by H. Low on Mt. Kina Balu in North Borneo. Apparently he was not quite certain of his determination, since he included in his record, as a synonym, the manuscript name *Mastigobryum Lowii* Sande Lac. When Stephani studied Low's specimens many years later he saw that they were distinct from *B. tricrenata* and described them as a new species under Sande Lacoste's manucript name.[20] The writer regrets that no specimens of *M. Lowii* have been available for study. Stephani's published descriptions and figures, however, supplemented by the figures in his unpublished Icones, give an excellent idea of the species and show that it is amply distinct, not only from *B. tricrenata*, but also from *B. fuscescens*. In distinguishing *M. Lowii* from the latter species the most striking differences are those derived from the leaf cells. In *M. Lowii* the cells in the basal region have robust and, in many cases, coalescent trigones, usually with truncate sides, and the narrow pits in consequence are clearly defined. The cells in the apical region are even more remarkable; the thickenings of the walls are uniform and fully as great as in the basal cells. According to Stephani, the species has thicker

[19] *Ann. Mus. Bot. Lugdano-Batavi*, 1 : 305. 1864.

[20] *Hedwigia*, 25 : 204; Pl. 3, Figs. 46–49. 1886. See also *Bull. Herb. Boissier II*, 8 : 756. 1908.

walls than any of its allies; the lumina of many of the cells are less in diameter than the thickness of the walls. In *B. fuscescens* the basal cells have much smaller trigones, which rarely coalesce; the pits are wide and less clearly defined; and the cells in the apical region have much thinner walls, with more or less evident trigones. *M. Lowii* is further distinguished by its strongly deflexed leaves, which are semicordate at the dorsal base.

Another Indo-Malayan species with which *B. fuscescens* might be compared is *B. Gaudichaudii* (Gottsche) Schiffn.[21] This species was based on specimens collected by Gaudichaud at Singapore, but has since been reported from Ceylon. Although the leaves of *B. Gaudichaudii* agree with those of *B. fuscescens* in general form and in various characters derived from the apical teeth, the foliar cells present certain distinctive features. In *B. Gaudichaudii* the trigones in the apical portion of the leaf are "nodulose," according to Stephani, and his figures represent them as circular. In *B. fuscescens* the corresponding trigones have straight or slightly concave sides with pointed rays. The underleaves, although not dissimilar in form, yield even more important differences. In *B. Gaudichaudii* the margins are subentire, and the cells throughout are thin-walled and hyaline. In *B. fuscescens* the margins are distinctly toothed, and the cells have thickened walls with more or less evident trigones. The writer's conception of *B. Gaudichaudii* is derived entirely from Stephani's descriptions and figures.

SECTION GRANDISTIPULAE

Bazzania intermedia (Gottsche & Lindenb.) Trevis.

Mastigobryum intermedium Gottsche & Lindenb. Spec. Hepat. Mastigobryum, p. 82; Pl. 22, Figs. 1–6. 1851.
Bazzania intermedia Trevis. Mem. Ist. Lomb., 13 : 415. 1877.

Plate XV, Figures 16–25

Waterfall of the Aek Sordang, Loendoet Concession, Koealoe, March 27, 1927, H. H. Bartlett 7096. A widely distributed species

[21] *Conspect. Hepat. Archipel. Indici*, p. 159. 1898. *Mastigobryum Gaudichaudii* Gottsche, in Stephani, *Hedwigia*, 25 : 7; Pl. 3, Figs. 4–8. 1886; *Bull. Herb. Boissier II*, 8 : 757. 1908.

in the Indo-Malayan region and known also, according to Stephani, from Samoa. The type specimens were collected in Java.

The plants in Professor Bartlett's material grew in depressed mats with little admixture. They are dull brownish green, with the younger parts rather pale. The shoots are mostly 2–3 cm. long and branch repeatedly, the apparent dichotomies being mostly 3–10 mm. apart. The stems show, in cross-section, a slight dorsiventral compression and are usually 0.25 0.3 mm. in width by about 0.2 mm. in thickness. The distinction between the unistratose cortex and the medulla (Fig. 16) is a little better marked than in most species of Bazzania, although the difference in the size of the cells is slight. The average diameter of the medullary cells, for example, is about 16 μ, and the radial width of the cortical cells averages about 18 μ. The cell walls are all more or less pigmented with brownish gray, although those in the interior of some specimens show a yellowish cast in the younger parts. The radial walls in the cortical layer are usually only 2 μ thick, whereas the other walls (including the outermost) are usually 4–6 μ thick. Sometimes, however, this contrast is scarcely apparent. Throughout the interior of a section pits can usually be demonstrated without much trouble.

The leaves, which tend to disappear completely or almost completely from the older parts of the stem, are imbricate but not deflexed. They lie, on the contrary, in a single plane and are widely divaricate, forming with the stem an angle of 90 degrees or a little more in the outer part. They vary in outline from ovate to ovate-linguiform and, on well-developed plants, are mostly 2–2.3 mm. long, 0.75–0.9 mm. wide at the base, 0.6–0.75 mm. in the middle, and 0.45–0.55 mm. at the apex. The margin is rounded at the dorsal base, arching partly or wholly across the stem, but scarcely beyond, and then curving gently outward; at the ventral base it is likewise rounded and then curves in such a way that it lies parallel with the dorsal margin. These curvatures cause the leaves to be slightly falcate. The broad apex is rounded to truncate and exhibits a considerable range of variation with respect to its teeth. At one extreme three large and sharp, subequal main teeth are present (Fig. 17);

at the other extreme perhaps a dozen smaller and more irregular teeth are formed (Fig. 18); and between these extremes are many intermediate conditions (Fig. 19). The main teeth, if such are distinguishable, are mostly four to six cells long and some bear smaller teeth on the sides. The smaller teeth, whether secondary to the main teeth or not, may consist of projecting cells (Fig. 21) or may be slightly more complex. Except in the apical region and its immediate vicinity the leaf margins are entire, or nearly so, throughout.

The vitta, although extending beyond the middle, is not clearly defined except in the basal portion. Its cells (Fig. 20) show the usual arrangement in longitudinal rows and are mostly 20 40 μ in length and 20–22 μ in width. The trigones, which rarely coalesce, have slightly concave to slightly convex sides, and their rays taper gradually, so that the pits are not sharply marked. Toward the base, where it is mostly ten to fifteen cells wide, the vitta is separated from the ventral margin by two to four rows of cells, and from the dorsal margin by fifteen to twenty rows. The cells along the dorsal and ventral margins average about 12 μ in width; those in the apical portion and in the region between the dorsal margin and the vitta, about 20 μ in diameter. Most of these cells (Fig. 21) have uniformly thickened walls about 4 μ thick, but the transition between this type of cell and the cells of the vitta with their distinct trigones is very gradual.

The underleaves of *B. intermedia*, which are approximate to slightly imbricate, are subquadrate to quadrate-obovate in outline and measure about 0.75 mm. in length and width. They narrow gradually toward the line of attachment, which is transverse, with a short downward curvature at one end. The apex is broad and truncate, in some examples showing a median cleft (Fig. 22) and in others not (Fig. 23); otherwise the margins are vaguely and irregularly lobed; the lobes (which are sharp or blunt) number about six. In addition to the lobes, the margin shows scattered crenulations or denticulations formed by projecting cells (Fig. 24). The underleaves are bordered by a hyaline band, mostly two to six cells wide toward the base and five to twenty cells wide in the apical portion. This band is composed of color-

less thin-walled cells (Figs. 24, 25). The basal median region is occupied by a group of rectangular cells with slightly thickened walls and scarcely evident trigones.

The hyaliform leaves are nearly 0.12–0.14 mm. in diameter, and the lower sterile leaves measure 0.15–0.2 mm. in length by 0.15–0.18 mm. in width. Their outline varies from broadly ovate to suborbicular, and they narrow slightly toward the rounded-truncate apex. In some specimens this is marked by one or two denticulations, but the margin is otherwise entire or nearly so. The cell structure of the scale leaves is similar to that of the underleaves; a basal area of green cells is bounded laterally and apically by a band of hyaline cells, but the cell walls are all slightly thickened.

Lindenberg and Gottsche's illustrations include figures of a female branch (with perianth) and two detached perichaetial leaves. They describe the perianth as pyramidal, contracted, and triplicate toward the apex and ciliate-dentate at the mouth. According to their statements, the innermost perichaetial leaves are quadrifid at the apex, but their figures show two or three main divisions with supplementary lobes or teeth on the sides. In the present material only two female branches, without perianths, have been demonstrated. The largest perichaetial leaf measures 1.5 mm. in length, 0.9 mm. in width at the middle, and 0.4 mm. in width in the upper part. It is composed of thin-walled, hyaline cells and is about one third cleft into two slender, long-ciliate divisions, with the lateral margins bearing in addition a few narrow lobes or teeth projecting forward. The male inflorescence is apparently still unknown. Stephani makes no mention of the sexual branches in his description of *B. intermedia*[22] and does not figure them in his unpublished Icones.

It should perhaps be noted that the leaves in the present material are even more irregular with respect to their dentation than those shown by Stephani in his Icones. They are in closer agreement, however, with the leaves figured by Lindenberg and Gottsche. Stephani's illustrations were based in part on specimens collected by Kurz on Mt. Salak, Java, and in part on specimens

[22] *Bull. Herb. Boissier II*, 8: 774. 1908.

collected by De Vriese in the Banda Islands. In all probability the slight differences they show might well come within the range of variation of a single species.

The writer has followed Stephani in placing *B. intermedia* in the section Grandistipulae; and yet, on account of the irregular dentation of the leaves, it might equally well be placed in the following section, the Serrulatae. In typical members of the Serrulatae, however, the three main teeth stand out distinctly, and the marginal serrulations are clearly of a subordinate nature; in *B. intermedia*, on the other hand, the transition between the larger and smaller teeth is usually more gradual, making it difficult to determine, in many cases, whether three main teeth are present or not.

Among the Grandistipulae it will be sufficient to compare *B. intermedia* with *Mastigobryum oblongum* Mitt.[23] of the Himalayas and *M. ceylanicum* Mitt.[24] of Ceylon and other parts of the Indo-Malayan region. These species are smaller than *B. intermedia*, their leaves are usually definitely tridentate, and any supplementary teeth that may be present are essentially like the others. They agree, however, in their linguiform leaves; in their leaf cells, which have trigones in the vitta and uniformly thickened walls in the apical portion; and in their underleaves, which are largely composed of hyaline, thin-walled cells.

SECTION SERRULATAE

Bazzania erosa (R. Bl. & N.) Trevis.

Jungermannia erosa R. Bl. & N. Nova Acta Acad. Leop.-Carol., 12 : 230. 1824.
Herpetium erosum Nees in Montagne, Ann. Sci. Nat. II, 17 : 16. 1842.
Mastigobryum erosum Nees in G. L. & N., Syn. Hepat., p. 229. 1845.
Bazzania erosa Trevis. Mem. Ist. Lomb., 13 : 415. 1877.

Plate XVI

Summit of Dĕlĕng Baroes, Karoland, June 21, 1927, H. H. Bartlett 8489b. The species was based on material from Java,

[23] *Journ. Linn. Soc. Bot.*, 5 : 106. 1861. [24] *Op. cit.*, p. 105.

collected by Blume, but is now known from other islands in the Indo-Malayan region and also, according to Stephani, from Samoa. Nees von Esenbeck comments on its great frequency in Java. No descriptions of the sexual branches have as yet been published, and the present material, although bearing male branches, is destitute of female branches.

The Sumatra specimens grew in depressed mats and are mixed with *B. loricata*. Their color varies from greenish brown to yellowish brown, becoming dull and grayish with age. The robust stems, which are sparingly branched, often attain a length of 9 cm. They show the usual slight dorsiventral compression and measure about 0.35 mm. in width by 0.25 mm. in thickness. A cross-section (Fig. 1) shows that the cell walls are very thick throughout and that they are everywhere more or less deeply pigmented with yellowish brown, being darker toward the periphery. The outermost cells are about 27 μ in tangential width, and the interior cells average about 21 μ in diameter; the outermost walls are mostly 10–16 μ thick and the interior walls 6–10 μ thick. Throughout the interior pits can easily be demonstrated. Although the peripheral cells are a trifle larger than the interior cells and have walls a little thicker, there is no clear differentiation into cortex and medulla.

The leaves, which are slightly or not at all deflexed, are somewhat imbricate and spread widely from the stem. They are narrowly ovate in outline and usually measure 2.4–3 mm. in length, 1.2–1.4 mm. in width at the base, and 0.4–0.6 mm. in width at the apex. The long axis is almost straight. The line of attachment (Fig. 2) extends upward for a short distance and then curves downward and outward. The margin is rounded to subcordate at the dorsal base, usually arching across the stem or a little beyond, and then extends outward in a straight or slightly curved line; it is similarly rounded or subcordate at the ventral base and extends outward subparallel with the dorsal margin. The apex is truncate and normally tridentate with subequal teeth (Fig. 3), which, however, are subject to variation. The median or dorsal tooth, for example, may be larger than the others (Fig. 4), or there may be one or two supplementary teeth. Except in the

basal portion the margin is minutely and irregularly serrulate. The serrulations, which attain their best development on the sides of the apical teeth (Fig. 7), consist of projecting cells, or (more rarely) of small groups of cells. If they are unicellular some of the cavities extend into the projections, but many fail to do so; the serrulations then consist of thickened cell walls only. Backward from the apex the serrulations tend to decrease in number and in size (Fig. 6) and may be reduced to rounded or flattened convexities. In the basal portion, where the serrulations are eliminated, there are sometimes vague sinuations or lobings (Fig. 2).

The vitta extends about half of the length of the leaf, but is not clearly defined. The cells show the usual arrangement in longitudinal rows (Fig. 5) and are generally 30–60 μ in length by 25–30 μ in width. The trigones are large and conspicuous, with convex or subtruncate sides, and longitudinal coalescences of trigones are frequent. These usually involve two or three trigones and may attain a size of 50 by 15 μ. The pits are broad and distinct, especially in the transverse walls. At the base of the leaf the vitta is mostly twelve to fifteen cells broad, but narrows upward; it is separated from the ventral margin by about eight rows of cells and from the dorsal margin by about twenty rows. Outside the vitta the cells are smaller and irregular in arrangement, but still show large trigones with frequent coalescences (Figs. 6–7). Most of the cells along the margin are 20–30 μ long and 10–15 μ wide; between the margin and the vitta they are slightly larger, measuring 30–40 μ in length and 20–25 μ in width. The marginal cells tend to be parallel, with their long axes forming an acute angle with the margin, but this tendency is not always apparent.

The underleaves, which are appressed to the stem and loosely imbricate, are plane or nearly so, subquadrate to subrectangular in outline, and usually 1–1.2 mm. long. Some are longer than broad (Fig. 8) and others broader than long (Fig. 9). The line of attachment is straight and transverse, and a more or less definite cordate or auriculate process is present on each side. The square or rectangular outline of the underleaf is somewhat ob-

secured by a series of blunt lobes separated by rounded to angular sinuses. Sometimes there are as many as eight or ten lobes, but they are often less numerous and may be vaguely defined. In addition to the lobes the margin shows a series of minute and irregular denticulations, each consisting of a projecting cell (Fig. 10); as in the leaves, some of the cell cavities extend into the projection and some do not. The cells of the underleaves are thick-walled throughout; the wall thickenings are essentially like those in the leaves.

The flagelliform branches are about 0.15 mm. in diameter and bear distant to approximate scalelike leaves. These leaves (Figs. 11–13) are attached by a broad, transverse line and are subquadrate to ovate, with the apex varying from truncate to acute. They are mostly 0.3–0.45 mm. long by 0.25–0.3 mm. wide and show rounded to subcordate expansions at the base. Some run out into a single sharp point (Fig. 11), but they usually bear two or (rarely) three more or less definite teeth at the apex (Figs. 12–13). Otherwise, the margin varies from entire to minutely and vaguely denticulate or crenulate. The thick-walled cells of the scale leaves are much like those of the leaves and underleaves.

The male inflorescences occupy branches which scarcely equal in length the subtending underleaves. The closely imbricate, monandrous bracts are in three or four pairs, and their margins are so strongly involute that the bracts appear almost terete (Fig. 14). In this condition they are mostly 0.4–0.6 mm. long and 0.3–0.4 mm. wide; when spread out flat, however, their actual width is mostly 0.5–0.6 mm. and their outline becomes suborbicular (Fig. 15). The broad apex is mostly two- to four-toothed, with sharp teeth; in their normal position these teeth are more or less connivent, so that it is difficult to see them clearly. Besides the apical teeth the margin (except close to the base) bears a number of minute and irregular denticulations, consisting of projecting cells.

The basal bracteole (Fig. 16) is broad and suborbicular, measuring about 0.6 mm. in length, but the others are relatively narrower (Fig. 17). In one of the inflorescences studied the second bracteole

measured 0.55 by 0.35 mm. and the third, 0.3 by 0.15 mm. The bracteoles are all more or less clearly bifid with sharp lobes and are otherwise irregularly denticulate or dentate. The cells of the bracts and bracteoles are thin-walled, except in the apical portions. Here the cell walls show irregular thickenings of various kinds (Fig. 18), but much less pronounced than in the leaves, and occasional walls remain thin.

The writer has followed Stephani in his interpretation of *B. erosa*, but most of the earlier writers understood the species in a much broader sense. Lindenberg and Gottsche, for example, accepting the views of Nees von Esenbeck, distinguished four varieties under *Mastigobryum erosum*, designating them by the letters α, β, γ, and δ, and illustrated the first three of these varieties on their plate.[25] In his preliminary synopsis of the genus Mastigobryum Stephani apparently understood the species in the same sense. In his monograph, however, he reserved the name *M. erosum*[26] for var. α and segregated vars. β and γ as distinct species. He apparently ignored var. δ altogether. For var. β he revived the old specific name "*spiralis*," calling the species *M. spirale* (R. Bl. & N.) Steph.;[27] to var. γ he gave the new name *M. desciscens* Steph.[28] These two species are known from Java only. Although closely allied to *B. erosa*, they are easily distinguished by their underleaves, which are reflexed at the apex and bordered by a band of hyaline cells.

Bazzania subserrulata, sp. nov.

Caespitosa, flavo- vel fusco-virens; caules parce ramosi; folia laxe imbricata, decurva, recte patula, falcata, anguste ovata, 2–3 mm. longa, 0.6–0.75 mm. lata, apice tridentato dentibus acutis, margine minute serrulato; cellulae parietibus validis, trigonis magnis; foliola laxe imbricata, subquadrata vel subrectangulata, subcordata vel subauriculata, minute denticulata

[25] *Spec. Hepat. Mastigobryum*, p. 99; Pl. 16. 1851.
[26] *Bull. Herb. Boissier II*, 8 : 858. 1908.
[27] *Op. cit.*, p. 857. *Jungermannia spiralis* R. Bl. & N., *Nova Acta Acad. Leop.-Carol.*, 12 : 231. 1824.
[28] *Op. cit.*, p. 862.

cellulis ubique parietibus validus; flores masculi ignoti; rami feminei breves; folia floralia tri- vel quadrijuga, intima ovata, profunde plurifida; perianthium longe exsertum, obtuse trigonum, apice contracto, plicato, longe ciliato.

Plants in depressed mats, greenish brown to yellowish brown, becoming duller and more grayish with age; stems as long as 9 cm., sparingly branched, the apparent dichotomies often as much as 3 cm. apart; leaves loosely imbricate, deflexed, widely spreading (when flattened out), the outer part forming an angle of 90 degrees or a little more with the stem, distinctly falcate, narrowly ovate, mostly 2 3 mm. long and 0.6–0.75 mm. wide, truncate at the apex and usually sharply and subequally tridentate, the margin irregularly and very minutely serrulate; leaf cells with large and often coalescent trigones, the vitta vaguely defined: underleaves loosely imbricate, plane or nearly so and appressed to the stem, subquadrate to subrectangular, mostly 0.5 0.7 mm. long, transversely attached and shortly subcordate or subauriculate at the base on each side, minutely denticulate and vaguely lobed along the margin, composed throughout of thick-walled cells: male inflorescence unknown: female inflorescence borne on a very short branch; perichaetial leaves in three or four series, the outermost suborbicular, about 0.5 mm. long, the innermost ovate, about 1.2 mm. long and 0.6 mm. wide, divided to beyond the middle into about six slender, ciliate divisions; perianth long-exserted, obovoid, about 3.5 mm. long and 1–3 mm. in diameter, bluntly three-keeled throughout most of its length, plicate and contracted in the apical portion, long-ciliate at the mouth.

Plate XVII

Central peak of Dělěng Pintoe, Karo Highlands, June 11, 1928, Carel Hamel & Rahmat Si Toroes 605, specimens received from H. H. Bartlett. Type in the herbarium of Yale University.

The material is almost free from admixture. A cross-section of the stem (Fig. 1) measures about 0.4 mm. in width by 0.3 mm. in thickness and thus indicates a slight dorsiventral compression. The contrast between cortex and medulla is perhaps a little more

striking than in *B. erosa*. The cells of the outermost layer are about 30 μ in tangential width and have very thick walls, those on the outside being mostly 12–16 μ thick; the cells in the interior average about 20 μ in diameter, and their walls are only 3–6 μ in thickness. There is also a slight difference in color; the walls of the interior cells are colorless or pale, whereas those of one to three layers on the outside are golden brown. Well-marked pits are not infrequent in the peripheral layers.

The leaves of dry plants are so strongly deflexed that they often meet on the ventral side of the stem; on moist plants the leaves, although still distinctly deflexed, are usually separate. These features recur in many other species of Bazzania. In the present species the dorsal and ventral margins of the leaves are curved and subparallel throughout the greater part of their length, in spite of the fact that the leaves taper slightly. In one leaf, for example, having a length of 2.1 mm., the basal width was 0.75 mm., the median width 0.6 mm., and the apical width 0.45 mm.; but the differences in width are often less pronounced. At the dorsal base the margin is rounded but scarcely cordate; it arches partly or wholly across the stem, but rarely beyond, and then curves outward. At the ventral base the margin likewise curves outward from a similarly rounded base. The apical teeth, although normally subequal and three in number (Fig. 2), are not infrequently unequal and may be increased to four. The teeth (Fig. 5) are very minutely serrulate; the serrulations consist of slightly projecting cell walls, into which the cavities may or may not extend. The serrulations occur very sparingly along the cell margins below the teeth and are even less conspicuous than in the apical region. Close to the base vague marginal sinuations, associated with slime papillae, can sometimes be demonstrated.

The indistinct vitta is similar to that of *B. erosa* and extends from the base of the leaves to the middle, or a little beyond. The cells, showing the usual arrangement in longitudinal rows (Fig. 3), are mostly 25–40 μ long and 20–25 μ wide. The trigones are large and distinct, with frequent longitudinal coalescences, some of the latter being 35 μ in length by 10 μ in width. The vitta is mostly

six to eight cells wide at the base, but narrows gradually upward. There are usually about four rows of cells between the vitta and the ventral margin and about fourteen rows between the vitta and the dorsal margin, but these numbers are subject, of course, to considerable variation. Along the margins (Fig. 4) the cells are mostly 12–20 μ long and 10–12 μ wide; they tend to lie subparallel, with their long axes forming an acute angle with the margin. In the other parts of the leaf, including the apical region (Fig. 5), the cells are mostly 25–30 μ long and 20–25 μ wide. Trigones, with frequent coalescences, are everywhere conspicuous.

The underleaves, as in *B. erosa*, are sometimes longer than broad (Fig. 6) and sometimes broader than long (Fig. 7). The marginal denticulations are irregular and usually consist, as in the leaves, of unicellular projections, into which the cell cavities rarely extend (Fig. 8). Some of the marginal irregularities are associated with slime papillae (Fig. 9). The underleaves are variable at the base, sometimes showing vague cordate or auriculate processes and sometimes not.

The flagelliform branches, which have a diameter of about 0.15 mm., bear scattered, appressed scale leaves. These are subquadrate to broadly ovate (Figs. 10–12) and measure, in most cases, 0.2–0.3 mm. in length. They occasionally run out into sharp points, but are much more likely to be broad at the apex, with two or three irregular teeth. Otherwise, the margin is vaguely and irregularly crenulate or denticulate and is scarcely dilated at the base.

The most characteristic of the perichaetial leaves are, of course, those of the innermost series. Instead of having two main divisions these leaves indicate a division into about six segments, the median segments being longer than the others (Fig. 13). The segments are further subdivided into delicate, subparallel laciniae or cilia, and sometimes as many as twenty of these are present. The cilia, which may be variously curved or contorted, occasionally show two cells side by side (Fig. 15) and not infrequently give off short projections (Figs. 15–16) or longer branches (Fig. 17). The intermediate bracts (Fig. 14), some of which are distinctly bifid,

are less complex than the innermost and show fewer and shorter divisions.

Throughout the greater part of its extent the perianth is unistratose. The cilia at the mouth are long and slender and resemble those of the innermost perichaetial leaves. In other words, they are often variously curved or contorted, one or (rarely) two cells wide, and sometimes sparingly branched. The cells of the perianth in the basal and median parts average about 28×20 μ; toward the apex they are longer and narrower, measuring 40–60 μ in length by about 16 μ in width; in the apical cilia they may be as much as 80 μ in length. Some of the cells in the vicinity of the mouth project as rounded or conical surface papillae, similar to those of *B. loricata*. The trigones in the walls of the perianth cells are smaller than those in the leaf cells, but often show convex sides and occasionally coalesce. The cells of the perichaetial leaves, with respect to their local wall thickenings, are much like those in the upper part of the perianth.

The serrulations on the leaves of *B. subserrulata* are so poorly developed that the assignment of the species to the section Serrulatae is perhaps open to criticism. At the same time the relationship of the species to *B. erosa* is so close that it would be illogical to separate them widely in a systematic arrangement. The deflexed leaves of *B. subserrulata* at once distinguish the species from *B. erosa*, in which the leaves tend to lie in a single plane, but the other differential characters are largely those of degree. The serrulations of the leaves, for example, are less well developed in *B. subserrulata* than in *B. erosa;* the leaf cells are smaller and their local wall thickenings are less pronounced; the underleaves are smaller, their marginal denticulations and lobings are less striking, and their basal cordate or auriculate expansions are less definite, or absent altogether.

It is unfortunate that the perianths and perichaetial leaves of *B. erosa* are still unknown. Comparison of *B. subserrulata* may be made, however, with *B. vaga* (De Not.) Trevis.,[29] a species

[29] *Mem. Ist. Lomb.*, 13 : 415. 1877. *Mastigobryum vagum* De Not., *Mem. Reale Accad. Sci. Torino II*, 28 : 295; Pl. 24. 1874. See also Stephani, *Bull. Herb. Boissier II*, 8 : 861. 1908.

which has sometimes been regarded as a synonym of *B. erosa*. According to De Notaris, the innermost perichaetial leaves are undivided or bifid, dentate on the sides, and ciliate at the apex. These features are clearly brought out in his figures and indicate that the leaves in question are very different from the plurifid and abundantly ciliate perichaetial leaves of *B. subserrulata*. The perianth of *B. vaga* is described as quinquefid at the mouth, with segments that are neither dentate nor ciliate. The numerous and crowded cilia at the mouth of the perianth in *B. subserrulata* present a very different appearance. *B. vaga* is known only from Borneo and was based on specimens collected by Beccari.

SECTION APPENDICULATAE

Bazzania paradoxa (Sande Lac.) Steph.

Mastigobryum paradoxum Sande Lac. Nederl. Kruidk. Arch., 3 : 419. 1854.
Mastigobryum dentatum Mitt. in Seemann, Fl. Vitiensis, p. 406. 1871.
Bazzania dentata Steph. Hedwigia, 32 : 210. 1893.
Bazzania paradoxa Steph. *Op. cit.*, 211. 1893.

Plate XVIII, Figures 1–11

Near triangulation pillar "D" on Dělěng Koetoe (near Kampong Goersinga), Karo Plateau, June 23, 1927, H. H. Bartlett 8536a. The species was based on material collected by Junghuhn in Java, but has since been reported from Sumatra and the Fiji Islands. *B. dentata* (Mitt.) Steph., which is here reduced to synonymy, has been reported only from Samoa, where it was originally collected by Powell (No. 92). Sande Lacoste's full descriptions and careful figures [30] give, in most respects, an excellent idea of *B. paradoxa*.

The specimens in the present collection grew in depressed mats with *B. tridens* and other bryophytes. Their color is a dull brownish, verging toward paler shades in the younger parts. The living parts of the shoots are mostly 4–5 cm. long, and the apparent dichotomies are usually infrequent, being separated from one another by a distance of 1.5–4 cm. The flattened stems are about

[30] *Syn. Hepat. Javan.*, p. 46; Pl. 9, Figs. 1–9. 1856.

0.45 mm. in width and 0.3 mm. in thickness, and a cross-section (Fig. 1) shows only a slight contrast between the peripheral and interior tissues. The thickened cell walls are everywhere more or less pigmented, from a pale yellowish gray in the interior to a darker brownish gray toward the outside. The cells of the outermost layer measure about 24 μ in tangential width, and the outermost wall is mostly 8–10 μ thick; the cells in the interior average about 22 μ in diameter, and their walls are mostly 4–6 μ thick. Pits are fairly abundant, especially toward the center of the stem.

The loosely imbricate leaves spread widely from the stem, the outer part usually at an angle of 90 degrees or more; in their natural position, however, they are strongly deflexed. When spread out flat they are ovate in general outline and slightly falcate, and they usually measure 2 2.6 mm. in length, 1 1.4 mm. in width at the base, 0.9–1.2 mm. at the middle, and 0.45-0.6 mm. at the apex. The margin at the dorsal base is rounded (Fig. 2), arching partly or wholly across the stem, but scarcely beyond, and then curving gently outward; at the ventral base the margin is irregularly dentate (Fig. 3) and often shows a distinct, dentate appendiculum. Beyond the basal portion the margin on each side of the leaf is subentire, showing no irregularities except vague sinuations, but it sometimes bears a few scattered short and blunt teeth, each formed by a projecting cell. The ventral margin converges slightly toward the dorsal and is usually less curved. The apex is distinctly and usually subequally tridentate, with sharp, straight teeth separated by acute or subacute sinuses (Fig. 4); as in other species, however, the teeth (Figs. 5–6) may vary in width and in direction, and may be more or less curved. They are mostly subentire, but some show a very few short denticulations.

Except in the basal region the vitta is vaguely defined, passing by imperceptible gradations into the adjoining foliar tissues. The cells in the most clearly differentiated part are mostly 40–70 μ long and 20 30 μ wide (Fig. 7). Their trigones are large and conspicuous, usually with convex or subtruncate sides, and frequently coalesce; some of the larger coalescences attain a size of 80 $\times$ 10 μ.

On the longer longitudinal walls it is sometimes possible to demonstrate subcircular intermediate thickenings, separated from the adjacent trigones by pits. In the basal portion the vitta is separated from the ventral margin by two to ten rows of cells, according to the dentation, and from the dorsal margin by fifteen to twenty rows. The cells in the apical portion of the leaf run a little smaller than those of the vitta, but usually measure 30–50 μ in length and about 20 μ in width. Along the margin toward the dorsal base (Fig. 8) the cells are mostly 20–30 μ long and 15 μ wide, and tend to lie subparallel with one another, with their long axes forming an acute angle with the margin. In all these cells the trigones are well developed.

The underleaves of *B. paradoxa* yield some of its most distinctive characters. They are loosely imbricate and usually plane, and closely appressed to the stem. Sometimes, however, they appear vaguely concave when seen from below, and their lateral margins may be slightly reflexed. The underleaves (Fig. 9) are subquadrate in outline, but are usually a little broader than long, if the length is measured from the line of attachment to the apex. Measured in this way they are mostly 0.7–1 mm. long and 0.09–1.2 mm. wide. The underleaves are deeply and irregularly cleft and show on each side at the base a large and complicated appendiculum. In the majority of cases there are four principal apical lobes, separated by narrow sinuses, with the median sinus often a little deeper than the others; in addition to these a more or less distinct lateral lobe can often be demonstrated on each side. The lobes tend to extend forward and are irregularly and coarsely dentate or ciliate; the number of teeth or cilia on each lobe is usually three or four. The appendicula, when well developed, are so large that they sometimes overlap below the transverse line of attachment. They are similar to the lobes, but extend outward or backward, and their teeth or cilia are still more numerous and irregular. The cells of the underleaves are everywhere thick-walled; the thickenings are essentially like those of the leaf cells.

The flagelliform branches are about 0.15 mm. in diameter. Their scattered scale leaves are subquadrate in outline, but are

usually a little longer than broad, measuring on well-developed plants about 0.25 by 0.2 mm. The apices vary from obtuse to truncate, sometimes showing a slight median indentation, and the cells are thick-walled, much as in the leaves and underleaves.

Sande Lacoste figures a female branch of *B. paradoxa*, together with a single perichaetial leaf dissected off, and describes the latter very briefly. In the present material a few female branches with unfertilized archegonia and very rudimentary perianths occur, although no male branches have been detected. The perichaetial leaves are in three or four series and show a marked increase in size in passing upward. Those of the innermost series are narrowly subrectangular in outline, when explanate, and are mostly 1.3–1.7 in length by 0.5–0.6 mm. in width. They are deeply divided into slender laciniae (Fig. 10), usually four, separated by narrow sinuses, with the median sinus often a little deeper than the others. Sometimes, however, only two or three main laciniae are present. The laciniae extend upward and tend to be parallel, but are often variously contorted and interwoven. They are mostly three to five cells wide at the base and taper to long slender points. The sides of the laciniae are variously dentate to short-ciliate, and the basal portion of the leaf is dentate in much the same way. The leaves of the second series (Fig. 11) are similar to the innermost leaves, although usually shorter and less elaborately toothed. Those of the succeeding series are much shorter and simpler. The cells of the perichaetial leaves have local wall thickenings much like those of ordinary leaf cells, but many of the thickenings are poorly developed in the apical and lateral portions of the leaves.

The perianths observed are composed of thin-walled cells and consist of nothing more than short sheaths extending scarcely beyond the archegonia. The mouths have a series of short denticulate cilia or laciniae, with occasional simple teeth interpolated among them. In addition to the marginal teeth, there are a few surface teeth or papillae, similar to those in *B. loricata*. In all probability these rudimentary perianths give but little idea of the normal form and structure of mature perianths.

In his descriptions of *Mastigobryum paradoxum* Sande Lacoste

makes no allusion to the teeth at the ventral base of the leaves, and his figure of a detached leaf represents the base as subentire. When Mitten proposed *M. dentatum* as a new species he compared it with *M. paradoxum*, but was apparently influenced, in his conception of the latter species, by Sande Lacoste's descriptions and figures. He gives, for example, as a distinguishing character of *M. dentatum*, the presence of a dentate lobule at the ventral base, thus implying that *M. paradoxum* lacks a structure of this type. According to Stephani,[31] who recognizes both species as valid, the leaves of *M. paradoxum* are denticulate or laciniate at the ventral base, whereas those of *M. dentatum* bear a crispate, sparingly toothed appendiculum. The writer finds that this rather vague distinction breaks down completely when numerous leaves of the two species in question are examined and compared.

The original specimens of *M. dentatum*, as represented in the Yale Herbarium, are a little more robust than the Sumatra specimens of *B. paradoxa*, and their leaves are relatively broader at the base and taper more abruptly toward the apex. The ratio between length and basal width emphasizes this difference. In *M. dentatum* this ratio is about 3 : 4, whereas in *B. paradoxa* it is only from 1 : 2 to 4 : 7. In other respects the specimens agree closely, and this is strikingly true of their remarkable underleaves. Since many species of Bazzania exhibit a considerable variation in the size and form of their leaves, even on a single plant, it seems inadvisable to recognize *M. dentatum* as valid on the basis of this single difference, and the writer feels justified in considering it a synonym of *B. paradoxa*.

Several species of the Appendiculatae are related to *B. paradoxa*. Perhaps the closest of these is *B. Macgregori* Steph.,[32] which was based on specimens collected by W. Macgregor on Panatinani (or Joanette) Island, east of New Guinea. In this species the leaves have an auricle at the ventral base, as do many leaves of *B. paradoxa*, but the auricle is entire, instead of being toothed. The species is further distinguished by its underleaves,

[31] *Bull. Herb. Boissier II*, 8 : 946. 1908.

[32] *Hedwigia* 32 : 210. 1893. *Mastigobryum Macgregorii* Steph., *Bull. Herb. Boissier II*, 8 : 942. 1908.

which are coarsely and irregularly spinose-dentate, rather than deeply laciniate.

Two other species of the Appendiculatae, *B. natunensis* Steph.[33] and *Mastigobryum Modiglianii* Steph., may be compared with *B. paradoxa*. The first of these was based on specimens collected by Micholitz on Great Natuna Island, west of Borneo, and has since been recorded from Borneo and New Guinea; the second is known from Sumatra, where the type was collected by Modigliani, and from Singapore. Both of these species present some of the features of *B. paradoxa* in a more intensified form. The leaves, for example, are more strongly dentate or ciliate at the ventral base and also have scattered but definite teeth throughout the greater part of their extent. The underleaves, too, are still more intricately divided than in *B. paradoxa*. The intricacy reaches a higher degree in *M. Modiglianii* than in *B. natunensis*, which occupies an intermediate position in this respect between *M. Modiglianii* and *B. paradoxa*.

Bazzania sumatrana (Sande Lac.) Steph.

Mastigobryum sumatranum Sande Lac. in Stephani, Hedwigia, 25: 234; Pl. 1, Figs. 7–9. 1886.
Bazzania sumatrana Steph. Hedwigia, 32: 209. 1893.

Plate XVIII, Figures 12–30

Summit of Dělěng Baroes, Karoland, June 21, 1927, H. H. Bartlett 8493. The species is known only from Sumatra, where the original specimens were collected by De Vriese in 1878.

The plants, according to the present material, grow in thin depressed mats with little admixture and vary in color from dull brown in the older parts to bright yellowish brown in the younger. Many of the stems attain a length of 10–12 cm., and the branching by apparent dichotomy is usually infrequent. Although two successive forks may be only 3 mm. apart they are, in most cases, much more widely separated and may be as much as 5 cm. apart. The slightly flattened stems are about 0.3 mm. in width and 0.2

[33] *Hedwigia*, 32: 210. 1893. *Mastigobryum natunense* Steph., *Bull. Herb. Boissier II*, 8: 941. 1908. *M. Modiglianii* is described on the same page.

mm. in thickness. A cross-section (Fig. 12) shows that the cells of the peripheral layer are about 26 μ in tangential width, whereas those of the interior average about 20 μ in diameter. The walls are pigmented with grayish brown, sometimes showing a yellowish cast toward the periphery. The outermost walls are mostly 8–14 μ thick, but those in the interior are mostly 4–8 μ. There is thus a slight contrast in size and in the degree of wall thickening between the cortical and medullary cells. Pits can easily be demonstrated throughout the section.

The leaves, which are loosely imbricate at the base, spread widely from the stem and are slightly, if at all, deflexed. They are more or less strongly falcate; the outer part often extends at right angles and sometimes, when the curvature is especially marked, lies subparallel with the stem. The leaves are narrowly ovate in outline and are generally 2–2.5 mm. long, 0.75–0.9 mm. wide at the base, 0.35–0.5 mm. wide in the middle, and 0.25–0.3 mm. wide at the apex. At the dorsal base the margin is rounded and usually entire, arching partly or wholly across the stem but scarcely beyond; sometimes, however, one or two irregular basal teeth or toothlike lobes are developed (Figs. 13–14). At the ventral base the margin may likewise be rounded (Fig. 15), but often shows a small and variable appendiculum (Figs. 16–19) with or without teeth, and sometimes one or two irregular teeth are present in addition to the appendiculum. The dorsal and ventral margins are subparallel in the outer part of the leaf and are either nearly straight in this position or variously curved. The apex is broad and truncate and sometimes has three, subequal, triangular teeth (Fig. 20). Usually, however, even when three teeth are present, they differ in size (Figs. 21–23), and in many leaves the apex shows only two teeth. Except for the apical and basal teeth the margin is entire, or vaguely sinuate.

The leaf cells in an indefinite area along the dorsal margin are irregular in their arrangement. Elsewhere they show a tendency to be in longitudinal rows (Fig. 24), so that the vitta, in which this arrangement is most pronounced, passes by imperceptible gradations into the surrounding tissues. The cells of the vitta in the basal part are mostly 25–50 μ long and 30–40 μ wide; the cells in

the apical part of the leaf are generally 20–40 μ long and about 25 μ wide; and the cells along the dorsal margin are about 17 μ in width. The trigones, which occur in all parts of the leaf, are large and conspicuous, with strongly convex-to-truncate sides, and the cell cavities in consequence are more or less stellate. Many trigones coalesce, and some of the larger coalescences in the vitta, which involve three trigones, attain a size of 35 by 10 μ. The pits are broad and persistent.

The loosely imbricate underleaves are slightly convex in the middle when viewed from below, but plane in the outer part and more or less appressed to the stem. They are subrectangular to ovate-oblong (Figs. 25–26) and are longer than wide, being 0.65–0.85 mm. long and 0.45–0.6 mm. wide. The apex is broad and truncate, and usually shows four to six sharp irregular teeth pointing forward and separated by sharp or blunt sinuses variable in depth. On each side of the underleaf three or four similar, but often blunter, teeth are present and these also tend to point forward. At the base on each side a small cordate or auriculate process, variable in form, can usually be demonstrated, but in some cases these processes are scarcely apparent, since the sides of the underleaf converge slightly toward the transverse line of attachment. The cells of the underleaves are essentially like the leaf cells.

The flagelliform branches are about 0.12 mm. in diameter, and the distant scalelike leaves, which are oblong to ovate, are of an average size (when well developed) of about 0.27 by 0.13 mm. The apices of the leaves are bluntly pointed to truncate and often develop two short and blunt teeth. The cells are everywhere thick-walled, much as in ordinary leaves.

The reproductive branches of *B. sumatrana* are not mentioned in the published descriptions of the species.[34] In the present material male branches occur in considerable abundance, but only one well-developed female branch was detected. The male branches are borne singly in the axils of the underleaves and are mostly 1–1.5 mm. in length by about 0.7 mm. in width. The

[34] In addition to the original description see Stephani, *Bull. Herb. Boissier II*, 8 : 948. 1908.

closely imbricate, monandrous bracts are in about six pairs, and the intact branch has a more or less distinct groove down the middle, between the two rows of bracts. The latter are shortly bidentate and complicate, the keel being rounded and strongly arched (Fig. 27). The bracts in the median part of the series are about 1 mm. long and 0.45 mm. wide in their normal complicate condition. The apical teeth are sharp and point forward; the sides of the teeth are minutely and irregularly denticulate or serrulate from projecting cells; and the margins of the bracts below the teeth are similarly denticulate or serrulate, except near the base. The bracteoles are convex when seen from below. Those from the middle of the series, such as the one figured (Fig. 28), are ovate in outline and measure about 0.9 by 0.4 mm. The apex is irregularly two- to four-toothed with sharp teeth, and the margin is otherwise irregularly denticulate or serrulate in the upper part. The cells of the male bracts and bracteoles, except at the base, are thick-walled, but the thickenings are less pronounced and more irregular than in the leaves. Some of the longer walls, for example, show intermediate thickenings between the trigones, and the pits sometimes become plugged on one or both sides by secondary deposits of thickening. Toward the base the walls gradually decrease in thickness.

The female branch studied bore about three series of perichaetial leaves. Those of the innermost series are ovate (Fig. 29) and measure about 1.5 by 0.8 mm. They show a deep median cleft between two subequal divisions, and each of these is further separated into from two to four, slender, parallel subdivisions extending forward. These are mostly one to four cells wide at the base, but the broader subdivisions soon taper, and all tend to be only one cell wide in the upper part. Occasionally, however, a division in the upper part may increase to two cells in width (Fig. 30). The cells of the perichaetial leaves have thickened walls, but the thickenings are not always apparent toward the tips of the subdivisions. In some cases the normal trigones are supplemented by rodlike thickenings projecting into the cell cavities (Fig. 30, cell at lower end), similar to those described in *B. loricata.* The mouth of the perianth is not very satisfactory

for study. It shows a dense cluster of slender cilia or laciniae similar to those of the perichaetial leaves, and some of the cells in the vicinity of the mouth project as short, surface teeth. The cells of the perianth, which are mostly in a single layer, are much like those of the perichaetial leaves.

The writer has seen no authentic material of *B. sumatrana*, but Stephani's descriptions and figures agree so closely with Professor Bartlett's specimens that they could hardly have been drawn from a different species. At the same time one slight discrepancy may be pointed out. If Figures 25 and 26 are compared with two figures of detached underleaves in Stephani's unpublished Icones, it will be seen that the margins of the latter are a little more sharply toothed. This difference, however, is so slight that it might easily come within a normal specific range of variation.

Stephani compares *B. sumatrana* with *Mastigobryum appendiculatum* Mitt. of the Himalayas.[35] The species resemble each other in the form of the leaves, in the character of the apical teeth, and in the wall thickenings of the leaf cells. In *M. appendiculatum*, however, the ventral basal process of the leaves and the basal processes of the underleaves are better developed and more complex than in *B. sumatrana*. They usually show a distinct constriction, and their margins are conspicuously dentate or lacerate. The underleaves are further distinguished by their vague apical sinuations and subentire margins.

SECTION VITTATAE

Bazzania vittata (Gottsche) Trevis.

Mastigobryum vittatum Gottsche, in G. L. & N., Syn. Hepat., p. 216. 1845.
Bazzania vittata Trevis. Mem. Ist. Lomb., 13 : 414. 1877.

Mossy jungle on the upper slopes of Dolok Soeroengan (as one ascends from Pagar Batoe), Habinsaran, May 18, 1927, H. H. Bartlett 7985. The species was based on specimens collected by Hasskarl in Java and was soon reported from other East Indian

[35] *Journ. Linn. Soc. Bot.*, 5 : 105. 1861.

islands. According to Stephani, its known range at the present time extends from Ceylon and Tonkin to Samoa and Tahiti.

The Sumatra material in the present collection grew in loose depressed mats and has some admixture with other bryophytes. The plants, which are dull green, slightly tinged with brownish, are considerably smaller than in any of the preceding species, the living portions being in general only 0.5–1 cm. in length. Branching by apparent dichotomy, the usual method of branching in Bazzania, is rare in *B. vittata*, and many of the stems examined failed to show it at all. Ventral branching from the axils of the underleaves, however, takes place frequently, and most of the ventral branches are leafy from the beginning, although the basal leaves are small and rudimentary. The flagelliform modification, which the ventral branches of Bazzania usually represent, is even rarer in *B. vittata* than the dichotomous type of branching.

The slender stems are mostly 0.1–0.2 mm. wide and 0.09–0.1 mm. thick, and cross-sections reveal but little differentiation between the cortical and the medullary cells. In the outermost layer the cells average about 18 μ in tangential and 16 μ in radial width, whereas the interior cells average about 14 μ in diameter. The outermost walls are only 2–3 μ thick, and the interior walls are even thinner, although they sometimes show slight thickenings at the angles. All the walls are pale brownish.

The approximate to loosely imbricate leaves spread widely from the stem at an angle of about 90 degrees. They are very slightly convex and not at all deflexed, so that they lie approximately in a single plane. On well-developed stems the leaves, which are ovate-oblong and slightly curved, are mostly 0.45–0.65 mm. long, 0.12–0.18 mm. wide at the base, and 0.25–0.35 mm. wide in the middle. The dorsal margin is distinctly curved and slightly rounded at the base, arching to about the middle of the stem, but scarcely beyond. The ventral margin usually meets the stem at an acute angle, without being decurrent; it may be almost straight, slightly convex, or curved in the form of a strongly flattened S. The apex is exceedingly variable. In what may be considered the most typical condition it is truncate and bears three short and bluntish teeth separated by very shallow sinuses,

with each tooth usually consisting of a single projecting cell. In many cases, however, one or more of the teeth may fail to develop, and the apex may then appear rounded, retuse, or subacute. Aside from the apical teeth the margins of the leaves are entire.

As the specific name implies, the vitta in the present species forms a striking feature of the leaves. Its cells are characterized not only by their relatively large size and by their arrangement in longitudinal rows, but also by their pale color. The vitta is mostly three or four cells wide at the base and tapers to a width of one or two cells at about the middle of the leaf, where its boundaries are less distinct than toward the base. It is separated from the ventral margin by three or four rows of cells and from the dorsal margin by twelve to sixteen rows. The cells of the vitta are mostly 20–30 μ in length by 15 20 μ in width, and their thin walls show small, occasionally coalescent, trigones with straight or slightly concave sides. Outside the vitta the cells are much smaller, averaging about 12 μ in diameter in the apical region and about 10 μ elsewhere. In all these cells minute trigones can usually be demonstrated. It is sometimes difficult to do so, however, on account of the densely and very minutely verruculose cuticle, which gives the leaf a frosty and semiopaque appearance.

The underleaves are distant to subimbricate, closely appressed to the stem and slightly convex when viewed from below. They are suborbicular to subquadrate, although most of them are a trifle longer than broad. Well-developed examples measure 0.2–0.25 mm. in length by 0.15–0.23 mm. in width. The straight or slightly bulging sides are entire or very vaguely crenulate, and the apex is rounded to truncate. In some cases the apex shows a slight median indentation, with crowded vestiges of slime papillae; in others it is vaguely crenulate or denticulate, with three or four small, irregular teeth; in still others one or two of the teeth are larger and more distinct. The cells throughout are thin-walled and hyaline, although very minute trigones are sometimes present, and the cuticle is minutely verruculose. The line of attachment is transverse and meets the line of attachment of a side leaf on one side; a slight connation is sometimes present. On the other side there is a little space between the side leaf and

the underleaf, and the latter sometimes curves downward for a very short distance.

The material studied has very few flagelliform branches and seems to be completely sterile. The inflorescence of *B. vittata*, in fact, is apparently still unknown. Lindenberg and Gottsche's figures give a clear idea of the vegetative organs.[36]

Var. *luxurians* (De Not.) Schiffn.[37] of *B. vittata* was based on a few scattered plants collected by Beccari in Borneo. In commenting on this variety, in connection with his description of the species (under the name *Mastigobryum vittatum*), Stephani expressed the idea that it might be specifically distinct.[38] In his unpublished Icones, where he has reproduced some of De Notaris' figures, he goes one step further and raises the variety to specific rank, but he has not given his new species nomenclatorial standing by actual publication. In the writer's opinion the characters of the variety, which De Notaris emphasizes, are insufficient to warrant a specific separation. The study of Beccari's actual specimens, however, might lead to a different conclusion.

Stephani assigns three species of the Vittatae to the Indo-Malayan region, in addition to *B. vittata*. Two of the species in question are *Mastigobryum integristipulum* Steph.[39] from Samoa, New Caledonia, Luzon, and Hawaii; and *M. luzonense* Steph.,[40] from Luzon. The writer has not seen the type specimens of either of these species, but has examined plants of each from the Philippines. These specimens were determined by Stephani and agree with his descriptions and with the figures in his unpublished Icones. They may, therefore, be considered authentic.

The type specimen of *M. integristipulum* came from Samoa

[36] *Spec. Hepat. Mastigobryum*, Pl. 2, Figs. 1–4. 1851.

[37] *Conspect. Hepat. Archipel. Indici*, p. 178. 1898. *Mastigobryum vittatum, luxurians* De Not., *Mem. Accad. Torino, Cl. Sci. Fis. Mat. II*, 28 : 293; Pl. 21. 1874.

[38] *Spec. Hepat.*, 3 : 531. 1909. The earlier fascicles of the third volume of Stephani's *Species Hepaticarum* were published in *Bull. Herb. Boissier* with two paginations, only the first of which is cited in the preceding pages; the later fascicles were issued as a separate publication by the *Herb. Boissier*, continuing the second pagination of the earlier fascicles.

[39] *Spec. Hepat.*, 6 : 470. 1924.

[40] *Op. cit.*, p. 472.

and, according to the Icones, was collected by Rechinger. The specimens studied by the writer, both of which are in the Yale Herbarium, are as follows: Canloon Volcano, Negros, April, 1910, Merrill 6842; and Mt. Maquiluig, Province of Laguna, Luzon, February, 1913, Robinson & Brown 17311. In the writer's opinion these specimens should be referred to *B. vittata*. It would be premature, however, in the absence of the type, to consider *M. integristipulum* a simple synonym of *B. vittata*, although Stephani's description and figures indicate a strong relationship. According to his account, *M. integristipulum* is a little more robust than *B. vittata*, the leaves are regularly three-toothed, the cell dimensions (except those of the vitta) are a trifle smaller, and the cell walls are thin throughout, without trigones.

The type specimen of *M. luzonense*, according to the Icones, was collected on the island of Luzon by Merrill, No. 9411. The specimen studied by the writer is in the Yale Herbarium and came from the same island. It was collected at Infanta, Province of Tayabas, in 1909, by Robinson, No. 9408. It shows that *M. luzonense* is amply distinct from *B. vittata*. The plants are considerably larger; the ventral branches are more frequently flagelliform; the leaves are relatively narrower, averaging about 1 mm. in length by 0.35 mm. in width; and the apices are more regularly three-toothed. According to Stephani, the median tooth is larger than the others and broadly triangular. This description certainly applies to the majority of the leaves, but the difference in size is not always pronounced, and other slight deviations from the typical condition sometimes occur.

The vitta is more yellowish than the rest of the leaf and is longer than in *B. vittata*, extending well toward the apex. It is, however, less clearly defined along the dorsal side. In the basal part it is mostly five or six cells wide, its cells average about 30 by 20 μ, and the well-developed trigones at their angles often have convex sides. In the apical part of the leaf the cells average about 20 μ in diameter and elsewhere about 15 μ, so that the cell dimensions are a trifle higher than in *B. vittata*. Except in the vitta the cell walls appear uniformly thickened, without trigones. The cuticle is mostly smooth, but sometimes, over the vitta, shows

faint and very delicate striolations. These detract but little from the transparency of the cuticle, and the parts beneath are clearly visible. The underleaves of *M. luzonense* are composed of hyaline cells with slightly thickened walls, much as in *B. vittata*, but the apex of the underleaves is more uniformly truncate.

The sections Fissistipulae and Cordistipulae (of Stephani's arrangement) are not represented in Professor Bartlett's collection, but there are two species belonging to the Inaequilaterae. This group, in the opinion of the writer, ought to be separated generically from Bazzania; it will form the basis of a future paper. The ten species discussed give a very inadequate idea of the rich representation of the genus Bazzania in the Indo-Malayan flora. Stephani reports over a hundred species from the region and a number of additional species from the islands of the Pacific.

The present study, however, brings out or emphasizes several points of more or less interest in connection with the genus as a whole and its taxonomy. Although only a few species were studied, these were sufficient to indicate that the tissues of the stem in Bazzania show comparatively little differentiation. Herzog, in his account of the histology of the stem in the leafy Hepaticae,[41] describes a similar condition in *Leptoscyphus Taylori* (Hook.) Mitt. (*Mylia Taylori* S. F. Gray), and his figure is not unlike the figures of stems in the present paper. In its stem structure Bazzania differs from the allied genus Lepidozia, in which the cortex is distinguished from the medulla by its distinctly larger cells. In certain other genera, such as Plagiochila and Scapania, in which the cortex is composed of several layers of thick-walled cells and the medulla of larger thin-walled cells, the contrast is even greater. To a certain extent there is a correlation in Bazzania between the thickness of the walls in the cells of the stem and the development of the local thickenings in the leaf cells.

The importance of the leaf cells in the taxonomy of Bazzania has long been recognized and is clearly shown in the preceding pages. Stephani pointed out many years ago that a band of

[41] In Linsbauer, *Handb. Pflanzenanat.*, 7[1]: 66; Fig. 59A. 1925.

larger cells occupied the median region of the leaves. This band represents the "vitta" of the writer's descriptions. In its most typical development a vitta is composed of cells which differ from the other leaf cells in their larger size, more regular arrangement, and different contents. This condition, which is manifested so clearly in such a species as *Diplophyllum albicans* (L.) Dumort., is realized in *Bazzania vittata* and its allies, in which the vitta is distinctly lighter in color than the rest of the leaf. In most species of Bazzania, however, the cells of the vitta do not differ from the other cells in color; they do so in size and arrangement only. In some cases, as already pointed out, the transition between the vitta and the surrounding tissue is very gradual, and a few species are known in which the median leaf cells are larger than the others, but not arranged in definite longitudinal rows. The leaves of such species could hardly be described as having a vitta at all. The cells of the vitta in Bazzania develop more or less distinct trigones. In the other cells similar trigones are often present, but in certain species the cells along the margin and in the apical region show uniformly thickened walls. The first condition is illustrated by *B. erosa*, the second by *B. intermedia*, and a somewhat intermediate condition by *B. tridens*.

The underleaves show an even greater diversity in their cell structure than do the leaves. Although in most species the cells are not essentially different from the leaf cells, so far as the local thickenings of the walls are concerned, there are a number of species in which the underleaves, either wholly or in part, are composed of hyaline and usually thin-walled cells. The hyaline cells sometimes form a marginal band of variable width, as in *B. loricata*, and sometimes involve the greater part or even the whole of the underleaf tissue, as in *B. tridens* and *B. pectinata*. The importance of these various types of cells in the underleaves, from a taxonomic point of view, has also been emphasized by Stephani. The scale leaves of the flagelliform branches agree with the underleaves in their cell structure, rather than with the leaves.

Our knowledge regarding the sexual branches of Bazzania is exceedingly incomplete and unsatisfactory. Many species are

still known in sterile condition only, and this is true even of certain abundant and widely distributed species. In other cases the branches of only one sex have been observed. The sexual branches, as a rule, are far more delicate in texture than the vegetative parts and often disintegrate to such an extent that their true structure can scarcely be demonstrated. On account of the difficulty involved in finding the sexual branches and in dissecting them for study, writers have been inclined to consider them unimportant from the standpoint of the taxonomist. It is doubtful whether this position is warranted. In a few cases, at least, the perigonial and perichaetial leaves, as well as the perianths, have yielded excellent differential characters.

Yale University

EXPLANATION OF PLATES XIII–XVIII

The figures were all drawn from Professor Bartlett's specimens.

PLATE XIII

Bazzania loricata (R. Bl. & N.) Trevis.

Fig. 1. Cross-section of stem. × 225

Fig. 2. Longitudinal section of stem, outermost layer at left. × 225

Fig. 3. Cells from apex of leaf. × 225

Fig. 4. Cells from side of leaf near apex. × 225

Fig. 5. Cells from dorsal side of leaf near base. × 225

Fig. 6. Cells from corresponding region of another leaf. × 225

Fig. 7. Cells from vitta of leaf near base. × 225

Fig. 8. Cells from middle of leaf, showing vitta at left. × 225

Fig. 9. Cells from apical part of underleaf. × 225

Fig. 10. Cells from side of underleaf near base. × 225

Figs. 11–12. Male bracts. × 50

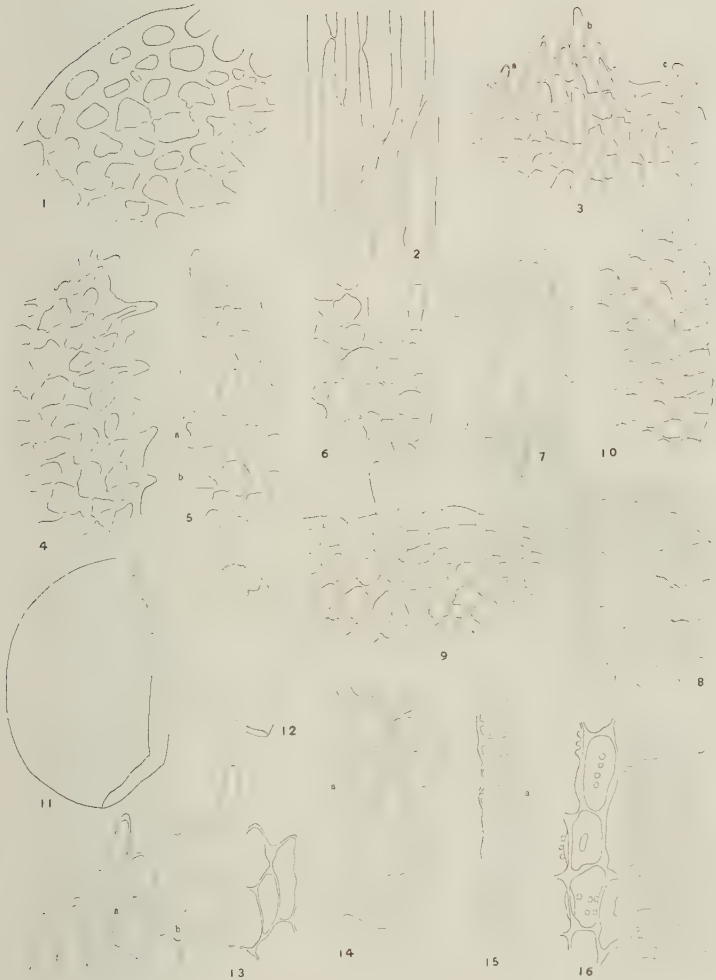
Fig. 13. Cells from apical portion of one of the innermost perichaetial leaves. × 225

Fig. 14. Cross-section of perianth at about middle. × 225

Fig. 15. Cross-section of perianth in upper part. × 225

Fig. 16. Cells from unistratose part of perianth, surface view. × 225

PLATE XIII



Bazzania loricata (R. Bl. & N.) Trevis.

PLATE XIV

Bazzania tridens (R. Bl. & N.) Trevis.

FIG. 1. Cross-section of stem. × 225

FIGS. 2–4. Apices of leaves. × 40

FIG. 5. Cells from vitta of leaf near base. × 225

FIG. 6. Cells from lower part of ventral side of leaf. × 225

FIG. 7. Apex of dorsal apical tooth. × 225

FIGS. 8–10. Underleaves. × 40

FIG. 11. Cells from apical part of underleaf. × 225

Bazzania pectinata (Lindenb. & Gottsche) Schiffn.

FIG. 12. Cross-section of stem. × 225

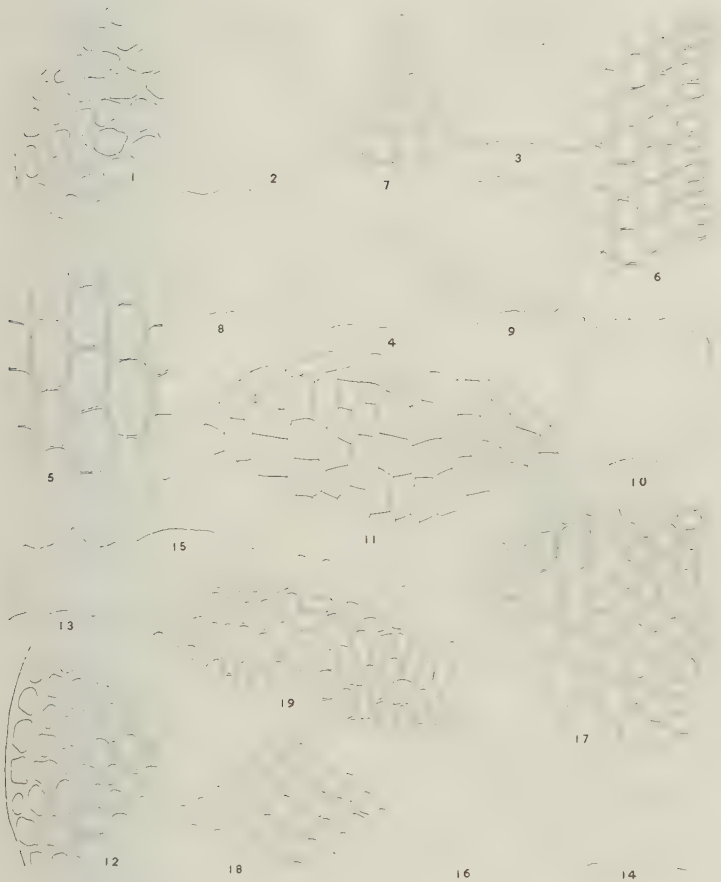
FIGS. 13–16. Apices of leaves. × 40

FIG. 17. Cells from ventral side of leaf near base, showing vitta at left. × 225

FIG. 18. Apical tooth of leaf. × 225

FIG. 19. Cells from apical part of underleaf. × 225

PLATE XIV



1–11. *Bazzania tridens* (R. Bl. & N.) Trevis.
12-19. *Bazzania pectinata* (Lindenb. & Gottsche) Schiffn.

PLATE XV

Bazzania fuscescens Evans

FIG. 1. Cross-section of stem. × 225

FIGS. 2–5. Apices of leaves. × 40

FIG. 6. Cells from vitta of leaf. × 225

FIG. 7. Cells from middle of ventral side of leaf, showing vitta at left. × 225

FIG. 8. Cells from middle of dorsal side of leaf. × 225

FIG. 9. Apex of dorsal tooth of leaf. × 225

FIGS. 10–14. Underleaves. × 40

FIG. 15. Cells from apical part of underleaf. × 225

Bazzania intermedia (Gottsche & Lindenb.) Trevis.

FIG. 16. Cross-section of stem. × 225

FIGS. 17–19. Apices of leaves. × 40

FIG. 20. Cells from middle of ventral side of leaf, showing vitta at right. × 225

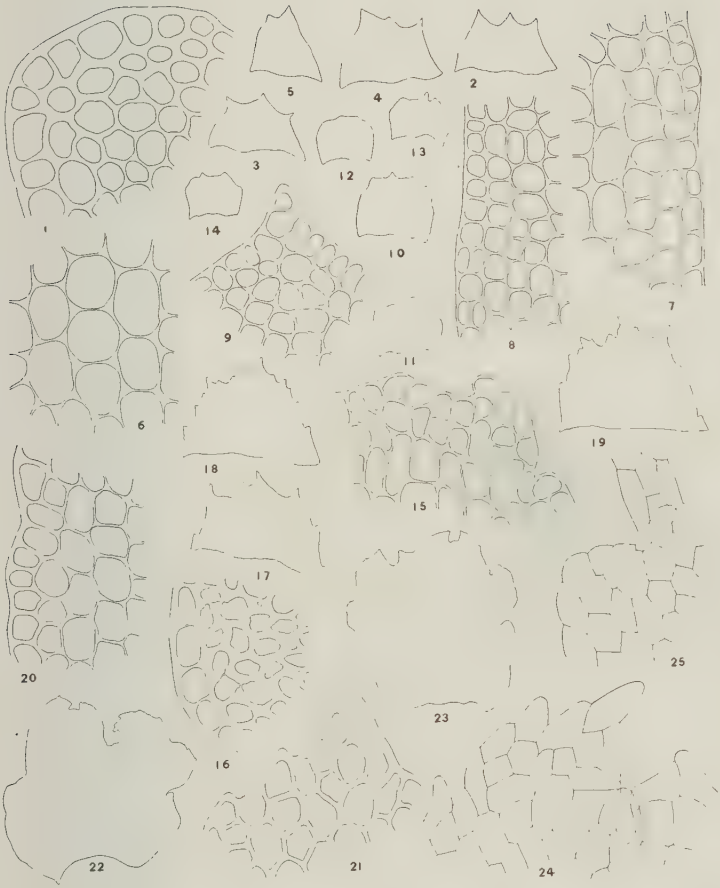
FIG. 21. Apex of ventral tooth of leaf. × 225

FIGS. 22–23. Underleaves. × 40

FIG. 24. Cells from apical part of underleaf. × 225

FIG. 25. Cells from side of underleaf. × 225

PLATE XV



1–15. *Bazzania fuscescens* Evans
16–25. *Bazzania intermedia* (Gottsche & Lindenb.) Trevis.

PLATE XVI

Bazzania erosa (R. Bl. & N.) Trevis.

FIG. 1. Cross-section of stem. × 225

FIG. 2. Base of leaf, dorsal view. × 40

FIGS. 3–4. Apices of leaves. × 40

FIG. 5. Cells from vitta of leaf. × 225

FIG. 6. Cells from ventral side of leaf in upper half. × 225

FIG. 7. Apex of ventral apical tooth. × 225

FIGS. 8–9. Underleaves. × 40

FIG. 10. Teeth from apex of underleaf shown in Figure 8. × 225

FIGS. 11–13. Scale leaves from flagelliform branch. × 50

FIG. 14. Male bract in natural condition. × 50

FIG. 15. Male bract spread out. × 50

FIGS. 16–17. Bracteoles from male branch. × 50

FIG. 18. Apex of right-hand division of bracteole shown in Figure 17. × 225

PLATE XVI

Bazzania erosa (R. Bl. & N.) Trevis.

PLATE XVII

Bazzania subserrulata Evans

FIG. 1. Cross-section of stem. × 225

FIG. 2. Apex of leaf. × 40

FIG. 3. Cells from vitta of leaf. × 225

FIG. 4. Cells from ventral side of leaf in upper half. × 225

FIG. 5. Apex of dorsal apical tooth. × 225

FIGS. 6–7. Underleaves. × 40

FIG. 8. Teeth from apex of underleaf. × 225

FIG. 9. Base of young underleaf. × 225

FIGS. 10–12. Scale leaves from flagelliform branch. × 50

FIG. 13. Perichaetial leaf of innermost series. × 40

FIG. 14. Perichaetial leaf of an intermediate series. × 40

FIGS. 15–17. Cilia from perichaetial leaf of innermost series. × 225

PLATE XVII

Bazzania subserrulata Evans

PLATE XVIII

Bazzania paradoxa (Sande Lac.) Steph.

FIG. 1. Cross-section of stem. × 225

FIG. 2. Dorsal base of leaf. × 40

FIG. 3. Ventral base of leaf. × 40

FIGS. 4–6. Apices of leaves. × 40

FIG. 7. Cells from vitta of leaf. × 225

FIG. 8. Cells from dorsal side of leaf near base. × 225

FIG. 9. Underleaf. × 40

FIG. 10. Half of perichaetial leaf of innermost series. × 40

FIG. 11. Perichaetial leaf of an intermediate series. × 40

Bazzania sumatrana (Sande Lac.) Steph.

FIG. 12. Cross-section of stem. × 225

FIGS. 13–14. Dorsal bases of leaves. × 40

FIGS. 15–19. Ventral bases of leaves. × 40

FIGS. 20–23. Apices of leaves. × 40

FIG. 24. Cells from middle of leaf, showing vitta at left. × 225

FIGS. 25–26. Underleaves. × 40

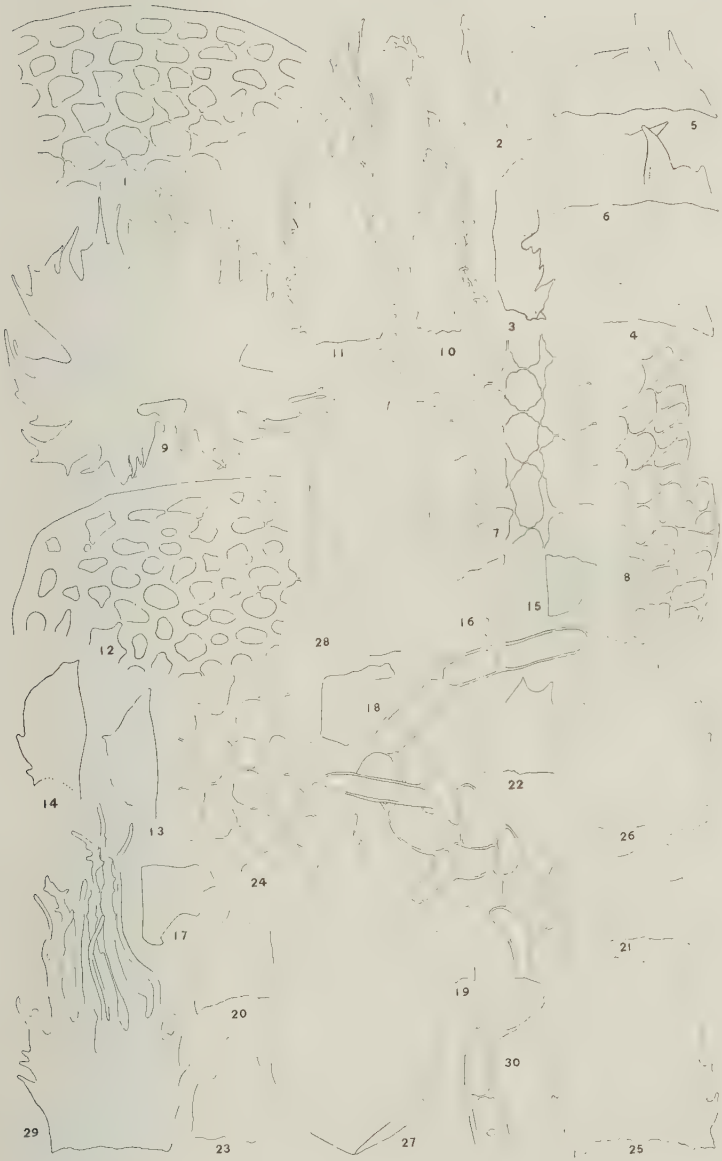
FIG. 27. Male bract. × 50

FIG. 28. Bracteole from male branch. × 50

FIG. 29. Perichaetial leaf of innermost series. × 40

FIG. 30. Apex of division of perichaetial leaf from innermost series. × 225

PLATE XVIII



1–11. *Bazzania paradoxa* (Sande Lac.) Steph.
12–30. *Bazzania sumatrana* (Sande Lac.) Steph.

SOME CHIPPEWA USES OF PLANTS

MELVIN R. GILMORE

IN THE past the Chippewa Indians, in common with all other tribes with which I am acquainted and from which I have sought information, had a very considerable body of lore concerning plants. Even at present all these people seem to have more knowledge of this subject than is common among white people.

Indians live more intimately with plants than most white people do and pay more attention to them. However well informed white people may have been on the indigenous vegetation in the old home in Europe, they have not yet made themselves well acquainted with the native plants of America. Even now, three and one-quarter centuries since the first English settlement in America, the European plants which accompanied the colonists from the Old World and established themselves in the new land are still better known to their descendants than are the native plants.

To be sure, among Indians, as among white people, there are some individuals who have given more attention to, and have better informed themselves concerning, plants than the majority. Yet a real knowledge of plants is diffused among the common people of the Indians more widely than among the whites. I find that Indians usually know more about plants as living things, and about their habits and requirements. Not only do Indians know the ways in which various plants serve human needs, but they also have a considerable knowledge of plant ecology. They generally know what factors of environment, such as soil, water content, sun and shade, are required by the different species.

I have found that Indians also observed closely the phenologic as well as the ecologic relations of plants. For example, they had learned that the most favorable time for stripping off outer layers

of birch bark without injury to the trees coincided with the time of the ripening of wild raspberries. This was also the best time for preparing strips of elm bark as roofing material for their houses. Among various tribes the time for planting corn was when the new oak leaves attained "the size of a squirrel's ear." Many examples might be adduced to show that certain phenomena in plant life synchronized with others in the cycle of seasons.

Indians respect plants as creatures possessing the mysterious and sacred attribute of life. They take them for use at need, for either food or healing or other purposes, religiously acknowledging their gratitude to the plant and to the Source of Life for the gift. This sense of debt is often expressed by a spoken prayer or by a token of sacrifice deposited at the place from which the plant is taken.

The information here recorded on uses of plants by Chippewas was obtained by interviews with a number of Chippewas unknown to one another and resident in different places, at Pinconning and Lapeer, Michigan, and in the Chippewa community near Sarnia, Ontario. I have made merely a fair beginning in assembling a list of species and their uses by this tribe. The uses are alimentary, medicinal, religious, esthetic, industrial, constructional, and magical. Certain plants had religious uses as incense and in symbolism; in esthetic uses some species served as perfumes, some as dyestuffs, stains, and cosmetics; in manufacturing of various kinds certain species of woods, barks, fibers, and resins were selected; in construction of boats and habitations different woods, barks, stalks, and leaves had specific purposes.

In addition to their knowledge of economic botany, plant ecology, and plant phenology Indians are generally well informed on plant geography, that is, they usually have a good knowledge of the range and distribution of species. They also have an elementary taxonomic system, based principally upon gross anatomy.

In the following pages I give a list of the native plants on which I have so far obtained information from the Chippewas. It contains one hundred and fifteen species grouped under forty-nine families. It does not include the cultivated plants, such as a number of varieties of corn in at least two of the main types, several

varieties of beans and pumpkins or summer squashes, and probably of sunflowers and "Jerusalem artichokes." All these cultivated plants originated far to the southwest of the Chippewa country; corn and beans in southern Mexico or Central America; and pumpkins perhaps in South America.

All the cultivated plants which the Chippewas possessed came to them through contact with other tribes. None of the plants indigenous to the country of the Chippewas had yet been brought into domestication by them, although there was some conscious dissemination and transplanting of useful and desirable species for the sake of convenience. It would seem that the idea of plant culture and control had first been put into practice in Central America and southern Mexico. Gradually, through the course of thousands of years, this tremendously pregnant idea, together with seed stock of corn, beans, and pumpkins, wandered farther and farther from the place of origin. As the practice of cultivation of those first crops migrated into new regions it no doubt stirred imagination and stimulated the application of similar principles to local species which in their natural state had been found useful and desirable. This stimulation had resulted in the addition of other species to the list of cultigens. Thus somewhere on the hither side of Mexico teparies (*Phaseolus acutifolius*), sunflowers (*Helianthus annuus*), and Jerusalem artichokes (*Helianthus tuberosus*) had been added. We find a little evidence that certain other species had also been brought into the company of cultivated plants and had later been rejected and abandoned. At all events, tentative experiments in plant control were under way in various regions by different tribes. The Chippewas, situated on the very periphery of the area of aboriginal agriculture, were touched in a measure by this idea of plant culture, so that they did practice to some extent the transplantation of a few indigenous species. Chippewa informants have told me of some such instances.

In noting the various uses made of plants I have employed the past tense unless I have definite knowledge of the continuance of such applications to the present.

TAXONOMIC LIST OF SOME INDIGENOUS PLANTS OF MICHIGAN, WITH THEIR CHIPPEWA NAMES AND USES

PHONETIC KEY

The spelling employed in representing the pronunciation of Chippewa words in this paper is intended to be most simple. The five vowels *a*, *e*, *i*, *o*, and *u* occur, with sounds as indicated below:

a as in *car*	*i* as in *marine*	*u* as in *rule*
e as in *they*	*o* as in *no*	

A macron above a vowel makes it long, as in the word *tōp*, in which the vowel has the sound of *o* in *pope*.

Consonants have the same sounds as English consonants unless modified by marks above them. A small superior *n*, as in *wika*^{n}, "calamus," signifies the nasalization of the preceding vowel. An inverted caret is a sign of aspiration, as in *miškodé*. Here the *š* sounds like *sh* in *shall*. The *č* in *čikadak* has the value of *ch* in *chin;* the *ž* in *skižik*, of *z* in *azure*.

EQUISETACEAE

Equisetum arvense L. Scouring rush, Horsetail. Jasibonskok, Aiankwošing

A decoction of the stems is drunk as a remedy for dysuria. It is said to be quick in effect.

From Adam Hart was received the information that a species of horsetail (*Equisetum arvense* ?), by him called *gežibnusk*, was used as a charm against the success of one's rival. If a man carried a few pieces of it in his pocket, it prevented good luck to his rival. An infusion of the plant sprinkled on a rival's traps would make them ineffective. The name *gežibnusk* is derived from *gežibwewe*, "to make a rustling sound," from the sound made by the stalks when rubbed together.

TAXACEAE

Taxus canadensis Marsh. American yew, Ground hemlock. Pebamabid-šingup

The name comes from *peba mabid*, "running on the ground," and *šingup*, "hemlock," which is equivalent to the English com-

mon name, "ground hemlock." This is one of the ingredients of the medicine which Chippewas call "the thirty-two medicine," because of the number of species it contains.

PINACEAE

Pinus strobus L. White pine. Wabaži^{n}guak

White-pine pitch, mixed with deer tallow, was used as a poultice for felons and similar inflammations.

Larix laricina (Du Roi) Koch. Tamarack. Pskignatik

Tamarack bark, with alder bark (*Alnus incana*), was steeped to make an infusion to be taken as a remedy for anemic conditions.

Abies balsamea (L.) Mill. Balsam fir. Pegyu-nagak-wizit

The name is derived from *pegyu*, "pitch," + *nagak*, "bark," + *wizit*, "that." This plant is also one of the ingredients of "the thirty-two medicine."

Tsuga canadensis (L.) Carr. Hemlock. Kagaga-winš

Hemlock bark was boiled to make a wash to clean steel traps of rust. It was said to be effective in preventing them from becoming rusted again. Strips of hemlock bark were used for the covering of wigwams. Young hemlock twigs were steeped to make a drink as a remedy for dysentery.

Thuja occidentalis L. Arbor vitae. Kizek, Kiskens, Kisgens, Songup

Twigs of arbor vitae were burned as a disinfectant to fumigate a house in which one was sick of a contagious disease, such as smallpox. Many years ago when smallpox first came to the Chippewas they moved into arbor vitae swamps and camped there during the period of the plague. Twigs were used in the vapor bath, and were burned for incense in religious ceremonies and as a common deodorant. The leaves were infused in hot water to make a beverage like tea; they were also used for perfume for the clothing and combined with ground hemlock for medicinal purposes. Ribs of canoes, as well as toboggans and handles of sturgeon spears, were made of arbor vitae wood.

Juniperus communis L. Shrub juniper. Ka^{n}winš

The twigs and leaves were boiled to make a drink to be taken as a remedy for asthma.

TYPHACEAE

Typha latifolia L. Cat-tail. Pokwiišk, Pokwiiškok

The name is derived from *pokwan*, "roof," + *wiiškok*, "grass." The leaves were used as mats for roofing wigwams. In making these mats the leaves were laid parallel, with one overlapping another, and were then stitched together with twisted thread of basswood fiber, or with the fiber of *Apocynum cannabinum* or of *Asclepias incarnata*. Thus overlaid upon one another like roofing boards, the leaves were quite effective in shedding the rain.

ALISMACEAE

Sagittaria latifolia Willd. Arrowhead. Čijak-kat
Sagittaria arifolia Nutt. Arrowhead. Čijak-kadens

The name is derived from *čijak*, "heron," + *kat*, "leg," i.e. "heron-leg." In the name of the smaller species *kadens* is diminutive of *kat*. These plants were said to have some medicinal uses, but my informant was unable to say for what ailments.

CYPERACEAE

Scirpus validus Vahl. Great bulrush. Nakun-aškok

The name is derived from *nakun*, "mat," + *wiiškok*, "grass." Bulrushes are used for weaving mats for the floors and walls; twisted threads of basswood fiber form the warp.

ARACEAE

Symplocarpus foetidus (L.) Nutt. Skunk cabbage. Šikag-buk

The root of this plant, in combination with several other species, is steeped to make a cough medicine.

Acorus calamus L. Sweet flag. Wika^{n}

The rhizomes of calamus, combined with the bark of *Xanthoxylon americanum*, the bark of the roots of *Sassafras variifolium*,

and roots of *Asarum canadense*, are steeped to make a remedy for colds, coughs, and bronchial troubles.

JUNCACEAE

Juncus effusus L. Soft rush. Pis-nakniskuns

The name is derived from *nakniskuns*, "rush," + *pis*, "fine." This rush was used for weaving little bags, pouches, and small mats such as table mats. Sometimes it was used in weaving larger mats, as much as three feet wide and three or four feet long.

LILIACEAE

Lilium philadelphicum L. Orange-red lily. Miškodé-pin

The name is derived from *miškodé*, "prairie" or "open plains," + *pin*, "bulb" or "tuber." Chippewas say this lily was always found on the lower levels of plains or open grasslands. The bulbs were boiled to make a poultice to be applied to wounds and contusions. These bulbs and the root of another plant called *nibnatugu*^{n}*s* were boiled together to make a plaster application for the bite of a dog. This was supposed not only to be a cure for the bite, but also to have the magic effect of causing the dog's fangs to drop out, so that "He could never bite anyone again."

Smilacina racemosa (L.) Desf. False Solomon's seal. Hu^{n}ksemin̆š

The root was dried, pulverized, and sprinkled on hot coals. The fumes were inhaled as a remedy for headache. A fomentation was made for relief from pain by applying to the painful part the powdered root placed on a hot stone.

Polygonatum commutatum (R. & S.) Dietr. Solomon's seal. Nebnegodek

The name is derived from *nebne*, "one-sided," + *godek*, "hanging," i.e. "hanging-one-sided." The root was supposed to be a preventive of certain diseases, such as measles. It was also burned for its pleasant fragrance, especially in the house.

Polygonatum biflorum (Walt.) Ell. Small Solomon's seal. Neb-negodek

The root was burned for its fragrance. When one burned it in a room before going to bed it insured sound sleep and caused one to awaken refreshed, rested, and feeling young, so it is said.

Smilax hispida Muhl. Cat brier. Manito minanga^{n}-winš

This plant was used in malicious magic. The vine was boiled with the powder obtained by pulverizing a certain kind of stone called *pisabik*. A mischief-maker would sprinkle this mixture upon the bed of a couple, thereby causing them to quarrel and separate. It was thought that the prickly character of the stem was transferred to the bed and irritated the couple, causing them to become ill-disposed toward each other.

IRIDACEAE

Iris versicolor L. Blue flag

The root of this plant, pounded to a pulp, was laid on a plantain leaf and applied to scrofulous sores for a cure. It should be said that this cannot be an ancient remedy, for *Plantago major* was introduced from Europe by white men and hence had previously been unknown to the natives of America.

SALICACEAE

Salix longifolia Muhl. Sandbar willow. Sasgob-minš

This willow was also called *kokbenognik keya*, "willow for making baskets." The springtime was the best season for weaving willow baskets of various forms and sizes. For this purpose the willows were cut and peeled, and then dipped in hot water to make them tough and pliable.

Populus balsamifera L. Balsam poplar. Ma^{n}-saté

The name is derived from *saté*, "poplar," "aspen," + *ma*^{n} "strange." The unopened buds of balsam poplar were gathered in early spring and boiled to extract the balsam. This was skimmed

off and then boiled with bear fat to make a salve which was applied to frost-bitten members and to sores and inflamed wounds.

MYRICACEAE

Myrica asplenifolia L. Sweet fern. Kba'agne-minš

Sprigs of this plant were commonly used to sprinkle water on the hot stones for the vapor bath. Sweet-fern leaves, with leaves of catnip (*Nepeta cataria*), were steeped to make an infusion to be used as a febrifuge. It should be noted that since catnip is not indigenous to America, but was introduced from Europe at the coming of the white men, it was unknown to Indians before that event. From the leaves of sweet fern there was made a table beverage like tea. They were also used for perfume and for medicine. Combined with the root of another plant not definitely known by my informant, dried leaves of sweet fern were burned as incense in religious ceremonies.

JUGLANDACEAE

Juglans cinerea L. Butternut. Pkanak

The bark of butternut roots was used to make a brown dye. It was said that no mordant was needed with this dye. Butternut sap, boiled down till it was thick and waxy and then mixed with cornmeal, was taken as a cathartic.

Juglans nigra L. Black walnut

Black walnut was also used to make a dark brown or a black dye.

BETULACEAE

Corylus americana Walt. Hazelnut. Pikanin-minš

Hazelnuts were used for food in season and also stored for winter.

Carpinus caroliniana Walt. Hornbeam. Ska'agon-minš

This tree was a favorite for use as main supporting posts for the ridgepole of the wigwam or tent, because of its convenient

size and suitable form, since it usually had a crotch just suited to hold the ridgepole and was tough and not liable to split.

Betula lenta L. Black birch. Winsik, Kade-wigwas

A mixture of the bark of black birch, beech (*Fagus grandifolia*), and red-osier dogwood (*Cornus stolonifera*) was regarded as a remedy for pulmonary trouble. A decoction of black birch bark was considered a specific for pneumonia, and also was said to be a remedy for diarrhea.

Betula alba L. Paper birch. Wigwas

Birch bark was stripped off at the time of the ripening of raspberries. It was then laid away, pressed out flat, until the next spring. When required for manufacture, especially in boat building, it was heated over a fire to make it pliable for shaping to the purpose.

Alnus incana (L.) Moench. Speckled alder. Tōp

The bark of speckled alder was boiled to make a bright red dye. When steeped with tamarack bark it served as a medicine for anemia.

FAGACEAE

Fagus grandifolia Ehrh. Beech. Šewe-minš

Beech bark, in combination with bark of black birch and of red-osier dogwood, was used in making a remedy for pulmonary trouble. Beechnuts were eaten, and people sought for stores of them which had been gathered and put away by chipmunks. These hoards saved the labor not only of gathering but also of shucking, and were certain to contain only sound nuts. The people had observed that chipmunks never stored any that were not good.

Quercus bicolor Willd. Swamp oak. Minšminš

The barks of swamp oak, hemlock, and soft maple (*Acer saccharinum*) were boiled together and the liquid was used to clean rust from traps. It was believed that after such cleansing they would not again become rusty.

Quercus spp. Oak. Mitigó-minš

Acorns of various species of oak served as food. Lye of wood ashes was used to eliminate the tannin. The lye was then leached out with water.

URTICACEAE

Ulmus americana L. White elm

Elm bark was peeled off at the time of the ripening of raspberries, for use as roofing material for the houses during the winter.

ARISTOLOCHIACEAE

Asarum canadense L. Wild ginger. Agabwen

Roots of wild ginger were slightly roasted and pulverized for use as a perfume. This powder was dusted into clothing and gave off its fragrance when damp. The roots were also used medicinally, being one of the five or six principal remedies for bruises and contusions.

POLYGONACEAE

Polygonum pennsylvanicum L. Heart-seed. Pebigumškike

The tops were steeped, and the infusion was taken as a cure for epilepsy. It is said that a case of epilepsy on the Sarnia Reservation in Ontario was cured by this means.

RANUNCULACEAE

Hepatica triloba Chaix. Hepatica. Pne-uzidi^{n}, Pne-obogo^{n}s

The name is derived from *pne*, "partridge," + *uzidi*^{n}, "foot." The roots of Hepatica and two other species of plants, sweet cicely (*Osmorhiza longistylis*) and the tall anemone (*Anemone virginiana*), are boiled together to make a remedy for amenorrhea. Hepatica was an ingredient in poultices for inflammations and bruises. According to the "doctrine of signatures," Hepatica, combined with some other plants, was used in making a remedy for liver ailments.

Anemone canadensis L. Anemone. Wabesgung

The name is derived from *wabes*, "numb," + *gung* "taste," from the effect which it has upon the mouth. The root of this plant, chewed slowly to a pulp and laid on a wound, serves as a styptic. For nasal hemorrhage the leaves, bruised and placed in the nostril, also act as a styptic. The roots are steeped to make a wash for obstinate, scabby sores, which stop bleeding and heal as it is applied. When this treatment is used the sore should not be bound up. This remedy prevents it from drying and cracking.

Caltha palustris L. Marsh marigold. Mi^{n}gde-beguk

The name is derived from *mi^{n}gde*, "wide," + *beguk*, "leaf." The leaves of this plant were cooked as greens for food. The roots were boiled and mashed to make poultices for stubborn sores. This is said to be a sure, and the only, cure known to the Chippewas for persistent running sores on the neck.

Coptis trifolia (L.) Salisb. Goldthread. Sau-tiskan

The roots were used to make a yellow dye.

Actaea alba (L.) Mill. White baneberry. Wapkadak

A decoction of the root was given as a remedy for convulsions in both children and adults.

BERBERIDACEAE

Podophyllum peltatum L. Mayapple. Sabšikan

Mayapples were considered a very palatable fruit.

LAURACEAE

Sassafras variifolium (Salisb.) Ktze. Sassafras. Menagwakeminš

The name is derived from *menag*, "fragrant," + *wak*, "root," + *minš*, "tree." Another name is *mesknagwekok*, "red bark." An infusion from the bark of the roots was taken as a "springtime medicine to thin the blood."

As a cooking flavor the leaves were put in meat soups, as bay leaves are used by white men. A tea made from the bark of the roots was considered a pleasant beverage.

Benzoin aestivale (L.) Nees. Spice bush. Kapak-minš

The word *kapak* in the name means "brittle" and refers to the brittleness of the wood of this shrub. The leaves were used medicinally and also to make a pleasant drink like tea. In cooking, the leaves were employed especially as a flavor for masking or modifying the taste of naturally strong-flavored meats.

PAPAVERACEAE

Sanguinaria canadensis L. Bloodroot. Meskwi-jibik

The name is derived from *meskwi*, "blood," + *jibik*, "root." The roots were dug in the fall, to be used as a red dye. It was said that sweet flag (*Acorus calamus*), dwarfed by growing on drier ground above the wet zone around ponds, was used for a mordant in dyeing with bloodroot. This plant was also used medicinally, but for what ailments my informant could not say.

SAXIFRAGACEAE

Ribes cynosbati L. Prickly gooseberry. Kauwe-šabu-min
Ribes gracile Michx. Smooth gooseberry. Šu^{n}s-šabu-min

Šabu-min is the name of the gooseberry; *kauwe* means "prickly"; *šu^{n}s* means "smooth." Both species were used as food.

Ribes floridum L'Hér. Wild black currant. Mik-min
Ribes rubrum L. Wild red currant. Šabu-min

Both black and red wild currants, fresh or dried, were used as food.

HAMAMELIDACEAE

Hamamelis virginiana L. Witch hazel. Nsakemižinš

The inner bark was used as an emetic, especially in cases of poisoning. It was also steeped and strained as a lotion for any skin trouble, and was especially valued as a wash for sore eyes.

ROSACEAE

Physocarpus opulifolius (L.) Maxim. Ninebark. Miskwazi-wušk

The name is derived from an herb with a medical use. The word *miskwazi* is the Chippewa name of the water-strider. *Wušk* is a Chippewa word for "plant" or "herb." It was thought that if a person drinking water at a pool accidentally swallowed a water-strider, an infusion made from the root of ninebark might serve as an emetic.

Spiraea salicifolia L. Meadowsweet. Demágene-minš

The name is derived from *demágenz*, "pipestem," + *minš*, "wood."

Amelanchier canadensis (L.) Medic. Juneberry. Negui-min

Juneberries, either fresh or dried for winter, were an important item of food.

Crataegus spp. Hawthorn. Minesga^{n}-winš

The root of a species of hawthorn, whose fruits "hang in clusters somewhat like the fruits of *nipin-minan*" (*Viburnum americanum*), was used, in combination with the wood of another species of tree which was not known by my informant, to make a remedy for consumption. A piece of the unidentified wood, of the thickness of a finger and the length of one finger joint, was cut up and steeped with a fragment of the root of Crataegus to make a drink for the patient. The root had to be one growing on the south side of the tree trunk.

Fragaria virginiana Duchesne. Strawberry. De-min
Fragaria americana Britton. Strawberry. De-min

The name *de-min* is compounded from the word *de*, "heart," + *min*, "berry," i.e. "heart-berry," in reference to the shape. Strawberries in season were an important item of the Chippewa dietary.

Rubus strigosus Michx. Wild red raspberry. Sku-min

The fruit, fresh or dried for winter, was used for food. A medicine for measles which failed to "break out" was made by boiling the roots or stems of the bushes.

Rubus occidentalis L. Wild black raspberry. Kadem-sku-min

The fruit of black raspberries, fresh or dried for winter, was used for food. A wash for sore eyes was made by boiling the roots.

Rubus alleghenienis Porter. Wild blackberry. Tetéga-min

Blackberries, fresh or dried for winter, served as food. The roots of the bushes, with the roots of the blueberry and of a species of wild rose, were steeped in water to make a tea to be taken as a remedy for diarrhea. They were also steeped to make a medicine to correct the condition of a pregnant woman threatened with miscarriage because of overexertion or a similar cause.

Rubus odoratus L. Purple-flowered raspberry. Tut'kag-minan

The fruit, fresh or dried for winter, was used for food.

Rubus triflorus Richards. Eyeberry. Skižgu-min

The name is derived from *skižik*, "eye," + *min*, "berry." The delicate and delicious fruit was used for food.

Rubus canadensis L. Dewberry. Šingábi-min

The fruit was used for food.

Rosa sp. Wild rose. Kenukatía-minš

The root of a wild rose was infused with the roots of blackberry and blueberry to make a remedy for diarrhea.

LEGUMINOSAE

Lathyrus palustris L. Wild pea. Pogotč-minjimin

The name is derived from *pogotč*, "wild," + *minjimin*, "pea." When full grown, the peas were shelled and cooked for food.

Apios tuberosa Moench. Rosary root. Pin

This plant was one of the most important vegetable foods of all the tribes living in its wide range. In the Chippewa language the word *pin* is a generic term signifying "tuber," and is applied to many tuberous growths, but always in combination with a modifying or definitive term, except in the case of this plant.

Apios is simply called *pin*, without any distinguishing term, because of its very high value and importance as a food, being considered the pin *par excellence*. Great quantities of apios formerly grew along the banks of the little river near which the town of Pinconning, Michigan, is situated. Because of the abundance of apios the Indians returned there every year to harvest a supply of the tubers. For this reason they called this locality *Pini-kaning*, which is to say, "the place of the *pin*." White men settling there called it by the Chippewa name, hence the present town name of Pinconning.

The common name, "rosary root," was given to this plant by the first French missionaries in eastern Canada when they observed the Indians harvesting the tubers. The tubers came from the ground connected in strings, so that they appeared to the missionaries like strings of beads. They spoke of them as "les racines des chapelets," "rosary roots."

Amphicarpa monoica (L.) Ell. Ground bean

This plant produces two forms of fruit, hence the generic name, which is compounded from two Greek words which signify "both" and "fruit." One form of the fruit is produced on the upper branches, which climb over other vegetation; the other is produced from branches which are prostrate on the ground. The fruits below push into the ground in the manner of peanuts, and are therefore called "ground beans." They are as large as lima beans and are very good eating. They formed an important item of food among all the tribes living within their wide range.

GERANACEAE

Geranium maculatum L. Wild geranium. Pesigunk

The name *pesigunk* means "bitter." The roots were steeped to make a remedy for diarrhea.

RUTACEAE

Xanthoxylum americanum Mill. Prickly ash. Agawak-minš

The name is derived from *agawak*, "prickly," + *minš*, "tree," "wood." One informant gave the name as *Kawago-minš*. The

bark of prickly ash was used in a number of medicinal preparations, one of which was to be taken as a hot drink for colds, coughs, and all pulmonary troubles. This was made by steeping a mixture of prickly ash bark, wild ginger root, bark of the root of sassafras, and rhizomes of sweet flag.

ANACARDIACEAE

Rhus glabra L. Smooth sumac. Pakwan-minš

My informant said that "the blossoms were chewed as a cure for sore mouth," but it was probably the acid fruits instead of the flowers which were used. They were also employed to make an acidulous drink which could be taken as a remedy for asthma. A dull red dye was made from these fruits. The leaves were dried and smoked. One informant stated that "curly bunches of leaves on top of the bushes" were used to make a mouth wash for sore mouth. An identified specimen of the "curly leaves" proved them to be the fruits of the shrub aborted and deformed from insect gall infestation. Sumac roots were steeped to make a drink to take for a cold, or as an emetic. For the latter purpose a large quantity was necessary.

Rhus vernix L. Poison sumac. Mijimniguns

Its virulent poison was well known, and the plant was avoided if possible.

CELASTRACEAE

Celastrus scandens L. Bittersweet.

The roots of bittersweet were cooked in animal fat, strained, and used as an ointment for cancer or any obstinate sore.

ACERACEAE

Acer saccharum L. Sugar maple.

The making of sugar from the sap of the sugar maple was one of the most important events in the year's cycle of industrial operations. Maple sugar was among the great staples in the domestic economy, and was a commodity of intertribal commerce, being traded to people of tribes in areas not possessing this tree.

Acer saccharinum L. Silver maple, Soft maple. Šigme-winš

Sugar was made from the sap of the soft maple also. Soft-maple bark was boiled to secure a wash for old, stubborn, running sores. The barks of soft maple, hemlock, and swamp oak were boiled together to make a wash to clean rusty steel or iron and prevent it from rusting afterward.

BALSAMINACEAE

Impatiens pallida Nutt. Pale jewelweed
Impatiens biflora Walt. Spotted jewelweed

The very succulent stems of jewelweed were bruised and applied locally to cure rash or other skin troubles.

RHAMNACEAE

Ceanothus americanus L. New Jersey tea. Kadegimnedu, Konjibik

To cure constipation, with bloating and shortness of breath, the roots of Ceanothus were steeped, and the patient drank freely of the infusion. It is said that the bruised root of this shrub is luminous in the dark. Roots of Ceanothus and roots or branches of the wild grape, roots of Hepatica, the bark of beech, the inner barks of sugar maple, black birch, and red-osier dogwood (*Cornus stolonifera*) were all steeped together to make a remedy for pulmonary trouble.

VITACEAE

Vitis spp. Wild grape. Šu-min, Šiwi-min

As stated in the preceding paragraph, the roots and branches of the wild grape were used with other ingredients to make a remedy for pulmonary trouble. The sap of grapevines was caught and used as a tonic to wash the hair. It is said that by using grapevine sap in this way "Indians used to have long, good hair."

TILIACEAE

Tilia americana L. Basswood. Wigobi-minš

Basswood was used to make dugout canoes, spiles for drawing maple sap from the trees into buckets in sugar-making time,

and many other articles of wood. Strips of bast from basswood were used for tying the poles of the framework of houses. Bast was boiled and rubbed on a stick to separate the fibers to be spun into thread for sewing, and into fine yarn for weaving beautiful bags, as well as into cordage of all sorts. Young twigs and buds were cooked for greens, or eaten raw.

THYMELACEAE

Dirca palustris L. Leatherwood. Čibagup, Jibagup

Bark of leatherwood is very tough and pliant, almost like leather, and so was very useful for tying and binding. The roots were used medicinally, having been steeped to make a drink for pulmonary troubles.

ARALIACEAE

Panax quinquefolium L. Ginseng. Šuniau-jibik

This name is derived from *šuniau*, "money," + *jibik*, "root." It has been so called because the white traders' demand for the root made ginseng a certain money commodity for the Chippewas. It was also considered by some as a good-luck charm if carried in the pocket.

Aralia racemosa L. Spikenard. Či-kadak

The root was used to make poultices for boils. It was also steeped to make a decoction to drive away "blue-tailed swifts," a kind of lizard, when these animals made themselves troublesome.

Aralia nudicaulis L. Wild sarsaparilla. Kada-ku^{n}s

The name means "little kada," as distinguished from *či-kadak*, "big kada."

UMBELLIFERAE

Osmorhiza longistylis (Torr.) DC. Sweet cicely. Segede bwens

If a hunting dog's sense of scent had become dulled, a decoction of the root of sweet cicely was made to wash out his nostrils. It was said that this treatment would restore his olfactory sense.

An infusion of sweet cicely root was taken by women as a remedy for amenorrhea.

CORNACEAE

Cornus stolonifera Michx. Red-osier dogwood. Meskwabi-minš

The bark was steeped to make a wash for curing eruptions caused by poison ivy, or by any other poison. It was also taken as a remedy for diarrhea.

Cornus alternifolia L. f. Dogwood. Mu^{n}s-minš

The bark was used medicinally, to bathe the eyes when bruised or bloodshot.

Cornus florida L. Flowering dogwood. Nemwatik

The inner bark of flowering dogwood, with several other ingredients (Sanguinaria, Asarum, Ostrya) was used to make a cough remedy.

Nyssa sylvatica Marsh. Pepperidge. M'gos atik

The name is derived from *m'gos*, "awl," + *atik*, "wood"; because the wood is so tough it was used to make awl handles, mauls, and war clubs since it would not split or check.

ERICACEAE

Cimaphila umbellata (L.) Nutt. Prince's pine, Pipsissewa. Yaskopteg

This plant, in combination with several other species, was used to make a remedy for gonorrhea in the initial stage.

Pyrola elliptica Nutt. Shinleaf. Ni^{n}begoskok, Yaskobgedek

This plant, together with two others which my informant was unable to name, was used for making poultices.

Gaultheria procumbens L. Wintergreen. Winsibog

Wintergreen leaves were used to make a pleasant beverage like tea, and also a cooking flavor. In combination with some other plants, unnamed by my informant, wintergreen was employed as a remedy for colds.

A "spring and fall medicine" was made from wintergreen, Mayapple, wild sarsaparilla, wild spikenard, burdock, dandelion, prickly ash, black cherry, sassafras, prince's pine, and black birch. Two plants of this list, it should be noted, are naturalized from Europe, namely, the burdock and the dandelion, and hence could not have been known to Indians in aboriginal times. It must be understood that Indians have been learning from whites and whites from Indians during the entire period of contact between the two races.

In making this "spring and fall medicine" the required parts of all these eleven species were boiled together to form a strong decoction. One gallon of this liquid was then boiled down to one half, and some whiskey was added in order to keep the preparation from spoiling. Everyone would take one tablespoonful three or four times a day through the spring and autumn "to keep the blood in good order."

Vaccinium spp. Blueberry. Minan

The fruits of several different species were gathered in season and used for food, either fresh or dried for winter. They were keenly relished and were used in large quantities and in a great variety of ways.

OLEACEAE

Fraxinus nigra Marsh. Black ash. Wisigak

The name means "bitter ash." The word *wis* signifies "bitter." Black ash is the species which is used for basket-making. Logs of the wood are beaten with mauls until the growth layers are loosened so that they can be separated. These thin sheets of wood are then cut into strips of the desired width to weave into baskets. The wood is used for fuel when a quiet fire is desired, for in burning this species does not crackle and shoot sparks as some others do. The bark is used to make a blue dye in a manner similar to the way in which blue ash is prepared.

Fraxinus americana L. White ash. Nitiminš

The name is derived from *nit*, "spear," + *minš*, "timber." Another name is *bo-yak*, which means "straight-grained ash." It

is called *nitiminš*, or "spear-timber," because it is the favorite wood used in making handles for fish spears.

APOCYNACEAE

Apocynum cannabinum L. Indian hemp, Dogbane. Sasáp-binš

The fiber of this plant was said to be the best that could be obtained for making fine cordage.

ASCLEPIADACEAE

Asclepias syriaca L. Common milkweed. Nini-winš

This was a common food plant. The sprouts, tender leaves, and tops, and the young green seed pods were cooked as greens.

Asclepias incarnata L. Swamp milkweed. Sasáp.

Good twine was made with the fiber of this plant.

LABIATAE

Monarda fistulosa L. Wild bergamot. Sasáp-kwanins

A wad of leaves of this plant, when chewed and placed in the nostrils, relieves headache. The tops of the plant were dried and used as a sternutatory for relief of colds. The leaves were placed in warm water baths for babies.

Mentha canadensis L. Wild mint.

Wild-mint leaves were used to make a pleasant beverage like tea, and to add flavor to certain meats in cooking. Mint was also employed medicinally as a carminative.

SCROPHULARIACEAE

Pedicularis canadensis L. Wood betony

The root of this species is said to be a remedy for anemic conditions. When dried and pulverized, it may be mixed with the food, or prepared as an infusion for drinking. It may also be eaten without any special preparation. It is said that one should be sure not to use the yellow species (*Pedicularis lanceolata* Michx.), for that is "the puff-adder's medicine," and if you

dig it "the puff-adder will follow you, blow on you, and then you will die."

RUBIACEAE

Galium aparine L. Goose grass. Pezukšku^{n}s

For rash or any other skin troubles dip stems of galium in cold water, bruise, and rub on the affected parts. Its use is similar to that of jewelweed.

Mitchella repens L. Partridge berry. Pne-minan

The name is derived from *pne*, "partridge," + *minan*, "berry." The whole plant was steeped and the infusion was used medicinally, but my informant was unable to say for what ailments.

CAPRIFOLIACEAE

Lonicera divica L. Honeysuckle. Šabankuk

In combination with two other shrubs this honeysuckle was used to make a diuretic medicine. The Chippewa names of the two other shrubs are *meskwabi-minš* (*Cornus stolonifera*) and *neakmižinš*. The identity of the last one was not learned. The medicine was prepared by taking as many honeysuckle stems fourteen or fifteen inches in length as the hand could grasp and placing them with five sticks each of *neakmižinš* and *meskwabi-minš*. The bark of all these was peeled off and steeped. The resulting infusion was then used by the patient instead of drinking water. It is said that this gave relief in cases of dysuria.

Diervilla lonicera Mill. Bush honeysuckle. Wežauškwagmik

An infusion of the bark of this shrub alone was used for an eye wash. In combination with three or four other species of plants it was a remedy for constipation.

Viburnum americanum L. Pembina, Cranberrybush. Nipin-minan

The fruits, both fresh and dried, were used as an acid sauce. They were employed as bait for snares set for snowshoe rabbits in times before guns had become common among the Chippewa

people. The roots were steeped to drink as a remedy for prolapsus uteri. Part of the treatment consisted of soaking a white cloth in an infusion of the roots and placing it in the vagina to pŭt the uterus back in place.

Viburnum lentago L. Sheepberry. Teta-minan

The sweet fruits of this species are eaten casually. The leaves are steeped to be drunk as a remedy for dysuria. A poultice made from the bruised leaves might be bound on the abdomen, over the bladder. It is said to take effect in a few minutes.

Triosteum perfoliatum L. Horse gentian. Moni^{n}swa^{n}

The informant gave the Chippewa name, but knew no use for the plant.

Sambucus canadensis L. Elderberry. Pipigwe-minan

The fruit was used for food, either in the fresh state or dried for winter. The steeped root was an emetic. Boys cleared the stems of the pith to make popguns.

CAMPANULACEAE

Campanula rotundifolia L. Bluebell, Harebell. Mekmi^{n}swa^{n}

This plant was used medicinally. In compounding "the thirty-two medicine" mentioned before, one of the ingredients was a bundle of the entire roots of three individual plants of this species.

COMPOSITAE

Eupatorium purpureum L. Joe-pye weed. Biaškagemesek

In combination with several other species of plants joe-pye weed was used as a medicine to counteract the bad effects of a miscarriage. As a cure for colds the tops were steeped and the patient inhaled the vapors.

Eupatorium perfoliatum L. Boneset. Šiabuksing, Šašabwaksing

Any part of this plant may be chewed and bound on a rattlesnake bite as a poultice to draw out the poison. The tops of

boneset and of wild bergamot (*Monarda fistulosa*) were boiled together to make a fomentation to be applied for rheumatism. Nicholas Plain, of Sarnia, Ontario, gave *piškagamisag* as the name. He said the root was used as a remedy to correct irregularities of the menses.

Rudbeckia hirta L. Black-eyed Susan. Wézawab-gonik

The name is derived from *wézawab*, "yellow," + *gonik*, "flower." The blossoms of this plant, together with a product of some other species of plant, called by the Chippewas *mekumi"swa"*, which was not seen and so not identified, were used to make poultices for babies.

University of Michigan

NOTES ON A COLLECTION OF MELASTOMATACEAE FROM CENTRAL AMERICA*

HENRY ALLAN GLEASON

THE recent collections of Professor H. H. Bartlett in Central America include twenty-two species of the family Melastomataceae, which have been submitted to me for identification. All the specimens come from the Belize and El Cayo districts of British Honduras or the Department Petén of Guatemala. Although many of the species are without special interest, as is always true of every general collection, two of them appear to be undescribed and seven others represent additions to the known flora of Central America. A list of the species, arranged in taxonomic sequence by genera, is given below, followed by a brief note on their phytogeographic relationships.

Acisanthera Bartlettii, sp. nov. — Caule erecto parce ramoso inferne glabro, superne glanduloso-pubescente; foliis sessilibus parvis erectis inferne ovatis superne ellipticis acutis glanduloso-ciliatis obscure 3-nerviis; bracteis linearibus; hypanthio campanulato cum sepalis triangularibus glanduloso; petalis obovatis; ovario 2-loculari.

Stems erect, simple, or sparingly branched, commonly somewhat thickened at the base, sharply 4-winged, smooth below, sparsely glandular-pubescent above, the internodes 4 15 mm. long; leaves sessile, very obscurely 3-nerved, glandular-ciliate, the submerged lower leaves rotund, deflexed, 2–3 mm. long, the middle ones spreading, narrowly ovate, 3–5 mm. long, the upper ones erect, narrowly elliptic, 2–3 mm. long, acute; flowers short-pedicelled, 5-merous, terminating the stem and its branches; hypanthium

* Based upon collections made by an expedition of the Herbarium and the Museum of Zoölogy of the University of Michigan, collaborating with the Department of Historical Research of the Carnegie Institution of Washington in a biological survey of the Maya area.

campanulate, 1.8 mm. long, freely glandular-pubescent; calyx tube not prolonged, the sepals triangular-subulate, 2.4 mm. long, acuminate, glandular-pubescent on the back; petals white, obovate, 5 mm. long, 3 mm. wide; stamens strongly dimorphic; filaments 2.3 or 1.9 mm. long, flat; large anthers fertile, subulate, the connective prolonged 0.6 mm. below the thecae and bearing two stout, rounded anterior lobes 0.7 mm. long; small anthers imperfect, funnelform, 0.2 mm. long, the connective prolonged about 0.2 mm.; ovary free, flattened, round, 2-celled; style 2 mm. long; stigma flat, barely wider than the style (Pl. XIX).

Type, Bartlett 11260, from Belize District, British Honduras, deposited in the herbarium of The New York Botanical Garden. *A. Bartlettii* is closely related to *A. limnobios* (DC.) Triana, but differs from it in its much narrower leaves, its stem glabrous below, and its smaller hypanthium and sepals. It is still more closely similar to *A. pellucida* Wright, in which the stem is more narrowly winged and the leaves are much broader, cordate, and somewhat clasping at base, ciliate, and conspicuously 5-nerved.

Acisanthera bivalvis (Aubl.) Cogn. — Belize District, 11215, 11235; a weedy plant becoming 4 dm. tall, often simple, but some of the more luxuriant plants freely branched above. This is apparently the first collection from Central America. *A. trivalvis* (Vahl) Cogn. differs essentially only in its 3-celled ovary and should, in my opinion, be merged with it. The two were not distinguished by Aublet, a careful observer, who published the first descriptions of both under the name accepted here.

Acisanthera quadrata Juss. — Belize District, 11269, 11380, 11382, 11388, 11411; an erect but freely branched herb 3–6 dm. tall. This is typically a plant of the West Indies, where it is common and widely distributed. It has also been collected at various stations in Central and South America. Since it often behaves as a weed, it is possible that it has been introduced into these outlying stations.

Pterolepis stenophylla, sp. nov. — Erecta ramosa, caule anguste alato parce strigoso; foliis subsessilibus lineari-lanceolatis 3-nerviis utrinque strigosis; floribus breviter pedicellatis 4-meris;

hypanthio penicillato-hirsuto eglanduloso; sepalis erectis triangularibus hypanthium aequantibus; antheris oblongis oblique lateque porosis, connectivo breviter producto antice bilobato; ovario apice setoso.

Stems slender, erect, freely branched, 3–5 dm. high, very narrowly 4-winged, sparsely strigose, especially on the wings, with geniculate hairs, the internodes mostly 3–5 cm. long; petioles scarcely differentiated, 1–2 mm. long; leaf blades firm, narrowly linear-lanceolate, acuminate, entire, cuneate to the base, 3-nerved, freely strigose above with slender hairs 1 mm. long or less and barely adnate at base, sparsely substrigose beneath with hairs about 0.4 mm. long, in size as much as 25 mm. long by 4 mm. wide; pedicels 1–2 mm. long; flowers numerous, 4-merous; hypanthium broadly campanulate, 3.2 mm. long to the torus, freely hirsute with penicillate hairs, their stout, reddish bases 0.4–1 mm. long, their total length 2–3 mm.; calyx tube not prolonged; sepals triangular, 3.2 mm. long, 1.9 mm. wide at the base, acute, glabrous on the back, conspicuously ciliate, tipped with a terminal bristle nearly 1 mm. long; petals obovate, rose color or magenta, about 5 mm. long; outer stamens: filaments flat, 2 mm. long; anthers oblong, opening by a wide ventro-terminal pore, the thecae 1.5 mm. long; connective barely prolonged between the thecae and the filament, bent at right angles and continued below the filament into 2 rounded lobes 0.3 mm. long; inner stamens: filaments 1.8 mm. long; anthers narrowly elliptic, the thecae 1.1 mm. long; connective stout, prolonged below the thecae about 0.3 mm. to the filament and beyond the filament into 2 very short lobes; ovary free, 4-celled, setose at the tip; style 3.7 mm. long (Pl. XX).

Type, Bartlett 11378, collected in the Belize District of British Honduras and deposited in the herbarium of The New York Botanical Garden. Bartlett 11259 and 11268, from the same locality, are conspecific.

The genus Pterolepis Miq. is primarily Brazilian. Of its thirty or more species only a quarter extend north of the Amazon and but three reach the shores of the Caribbean; one is endemic to Mexico and Central America. The species were grouped by Cogniaux chiefly according to the structure of the anthers,

supplemented by various vegetative characters. Under his system *P. stenophylla* appears to be related to *P. paludosa* Cogn., *P. maritima* (St. Hil.) Cogn., and *P. glomerata* (Rottb.) Miq., all of which have much larger flowers and wingless stems with a different type of pubescence. In general habit it resembles *P. saturejaeformis* Cogn., a Brazilian species with simple hypanthial hairs and glandular pubescence. The widely distributed *P. trichotoma* (Rottb.) Cogn. has a greatly prolonged connective; the equally common *P. pumila* (Bonpl.) Cogn., already known from Central America, has a longer connective, much broader leaves, shorter sepals, and glandular pubescence. *P. exigua* (Naud.) Triana, the endemic species of Central America and Mexico, is almost unbranched, with oval leaves and much shorter sepals.

Tibouchina longifolia (Vahl) Baill. — El Cayo District, 11707; a shrub as much as 2 m. tall. It is the commonest species of the genus, distributed throughout tropical America from Mexico to Bolivia and ranging from sea level to altitudes of several thousand feet.

Leandra mexicana (Naud.) Cogn. — Belize District, 11343; a shrub 2 m. tall. This is a typical and common species of Central America, often at considerable altitudes, and extends southward into Colombia.

Conostegia xalapensis (Bonpl.) Cogn. — El Cayo District, 11550, 11663; Belize District, 11407; noted as a shrub 6–18 dm. tall. This is another typical species of Central America from southern Mexico southward, extending also into Colombia and eastward into Cuba.

Miconia albicans (Sw.) Triana. — Belize District, 11295; El Cayo District, 11862, 13115, 13121. This is one of the commonest and most widely distributed species of the huge genus, ranging from sea level to high altitudes in the Andes, and from Bolivia and Paraguay through Central America and the West Indies to Mexico, preserving a remarkably constant structure throughout.

Miconia ambigua (Bonpl.) DC. — Dept. Petén, 12807; a small tree. The species has been considered to be primarily

West Indian, extending also to the coast of Venezuela; this is the first record from Central America known to me. Its previously known range coincides almost precisely with that of the related *M. virescens* (Vahl) Triana. The two have been differentiated chiefly on the basis of foliage characters; our species has larger leaves with five nerves, whereas *M. virescens* has smaller leaves with only three nerves. It is very doubtful whether the two should be kept separate.

Miconia argentea (Sw.) DC. — Belize District, 11329; El Cayo District, 11540; a typical species of Central America, ranging from southern Mexico to Panama and easily distinguished by the silvery-tomentose lower surface of its large leaves.

Miconia Chamissois Naud. — El Cayo District, 11657; a shrub 8–12 dm. tall. The species is abundant in central and southern Brazil, becoming less common to the north. This is apparently the first record of its presence in Central America. Although the leaf shape and venation are fairly distinctive, the chief diagnostic character of the species is the structure of the anther, and it is possible that Central American specimens have been previously collected and distributed under a different name.

Miconia ciliata (Rich.) DC. — Belize District, 11299, 11391; El Cayo District, 11679; a shrub 6–20 dm. tall. It is a common and widespread species, ranging from Central Brazil across South America and north to the West Indies and Mexico, but always most abundant at low altitudes.

Miconia impetiolaris (Sw.) Don. — Dept. Petén, 12327, 12634; El Cayo District, 11543; a small tree as much as 8 m. tall. It is a common species of Central America and the West Indies, extending southward, but in smaller numbers, to Bolivia.

Miconia oinochrophylla Donn. Sm. — El Cayo District, 11722; a shrub 3 m. tall. The inflorescence is red, the fruits are purple, and the leaves purple beneath, the last feature suggesting the specific name. It was originally collected at Livingston, Guatemala, in 1905 and is otherwise known to me only through a recent collection by Killip and Smith, at low altitudes in northern Colombia (Pl. XXI).

Miconia obovalis Naud. — Belize District, 11311; a shrub.

Cited specimens of this species indicate a range from Brazil to the West Indies and Central America, a distribution about coincident with that of *M. prasina* (Sw.) DC. It is entirely probable that the two species have sometimes been confused, and indeed possible that a careful study of the range of structural variation in *M. prasina* will reveal that the two species should be combined or the two together redivided according to more dependable characters which are as yet unknown.

Miconia pteropoda Benth. — El Cayo District, 11773; a shrub 2.5 m. tall. This species is also closely related to *M. prasina* and *M. obovalis*, and like them may stand or fall after a careful study of the group has been made. It has been known to me heretofore only from the Amazonian forests, but is reported from Panama.

Miconia stenostachya DC. — El Cayo District, 11930; a shrub 8 dm. tall. The species is closely related to *M. albicans* and resembles it in general habit. It has a similar broad distribution, extending from Mexico and the West Indies to Bolivia and southern Brazil, but usually at low altitudes.

Miconia subnodosa Triana. — El Cayo District, 13083. This species, long among the more obscure members of the genus, was originally collected by Triana on the west coast of Colombia, and so far as it is known to me has not been detected since until the present collection. Two specimens of Triana's original collection in the herbarium of The New York Botanical Garden afford opportunity for a precise comparison, which leaves no doubt about the identity of our plant. Both collections are from the lowlands, and the species may be found in the future at other intermediate stations (Pl. XXII).

Clidemia dependens Don. — Belize District, 11302, 11377; El Cayo District, 12978; a shrub as much as 18 dm. tall. It is a widely distributed species at low altitudes, ranging from southern Brazil and Bolivia through the West Indies and Central America to Mexico.

Clidemia novemnervia Triana. — Belize District, 11414; a shrub 1.2 to 2.5 m. tall. This is another species typical of the Amazonian forests, where it is fairly common and widely distrib-

uted. It has also been reported from Panama and the West Indies, but this is the first collection known to me from Central America proper.

CLIDEMIA RUBRA (Aubl.) Mart. — Belize District, 11294, 11386; El Cayo District, 11666, 11667; a shrub rarely exceeding 6 dm. in height, or often nearly herbaceous. It is exceedingly common in the Amazonian lowlands of South America and extends northwestward through Central America to southern Mexico, mostly at low altitudes.

CLIDEMIA STRIGILLOSA (Sw.) DC. — Belize District, 11300; El Cayo District, 11931; a shrub as much as 18 dm. tall. It is a lowland species, hitherto known from the West Indies and Amazonian South America.

Considering now the broader aspect of geographical distribution of the twenty-two species of the family represented in the collection, we find that they may be placed in four geographic groups, that seven of them are here reported for the first time from Central America, and that two are new species. These must naturally be considered as endemic until further collections show that they have a wider range.

Those now reported in the region for the first time are:

Miconia ambigua	Miconia subnodosa	Clidemia novemnervia
Miconia Chamissois	Acisanthera bivalvis	Clidemia strigillosa
Miconia pteropoda		

The four geographic groups follow in order of sizes:

1. Species of wide distribution in the American tropics, ranging from well south in South America through the West Indies and in many cases extending north to Mexico, mostly at low altitudes:

Miconia albicans	Miconia obovalis	Clidemia rubra
Miconia ciliata	Miconia stenostachya	Clidemia strigillosa
Miconia impetiolaris	Clidemia dependens	Tibouchina longifolia

2. Species primarily Central American, but in at least four cases extending somewhat beyond this region into adjacent territory:

Miconia argentea	Acisanthera Bartlettii	Leandra mexicana
Miconia o nochrophylla	Conostegia xalapensis	Pterolepis stenophylla
Miconia subnodosa		

3. Species primarily Amazonian:

Miconia Chamissois	Acisanthera bivalvis
Miconia pteropoda	Clidemia novemnervia

4. Species primarily West Indian:

Miconia ambigua	Acisanthera quadrata

The presence of seven typically Central American species is of course to be expected. It is perhaps somewhat surprising that the proportion is not greater, but many more would have been included if the collecting localities had reached to higher elevations in the mountains to the west. More noteworthy is the presence in Central America of nine species of very broad distribution through the American tropics, and of four species heretofore considered restricted to the Amazonian forests. It has long been known that Amazonian plants preponderate in the coastal flora of the Guianas, that a considerable number reappear near the mouth of the Magdalena River in Colombia, and that others have already been collected on the coast of British Honduras. Standley, in his recently published flora of the Lancetilla Valley in Honduras, has already called attention to the condition and says that his flora "will be found to contain some mention of a large proportion of the commoner plants that inhabit southern Mexico, the West Indies, and even northern South America."

This distribution leads us to two phytogeographical conclusions which may now be placed on record. First, the flora of the American tropics includes a large number of species which are so broadly adapted to the environment that they range through all or almost all the lowlands from Brazil to Mexico and are quite independent of the usual floristic segregation of the plant life into definite phytogeographic groups, as is normally expected in such a large region. Second, various members of the Amazonian flora have such good means of dispersal or have had such a continuous route for migration that they have spread far beyond the accepted limits of the Amazonian floristic region.

The New York Botanical Garden

PLATE XIX

Acisanthera Bartlettii Gleason. Type. × 1

Pterolepis stenophylla Gleason. Type. × ½

Miconia oinochrophylla Donn. Sm. × ½

Miconia subnodosa Triana. × ½

AGARICS COLLECTED IN THE VICINITY OF ROCK RIVER, MICHIGAN, IN 1929 *

CALVIN H. KAUFFMAN AND ALEXANDER H. SMITH †

THE agarics of the Southern Peninsula of the State of Michigan have been studied intensively over a period of about twenty years. During this time occasional collecting expeditions have been made into the Northern Peninsula, but as a whole the agaric flora of that region has been none too well known. Most of the previous collections had been made during the summer months, so that a study of the autumn forms seemed very desirable.

With this in mind a short expedition into the Upper Peninsula was organized. Since intensive studies on various groups of fungi had previously been made at a camp located at the mouth of Rock River (14) and since this locality offered a wide variety of habitats, it was without question a most desirable location for continued study. The general topography of this area has been described in a previous paper (14), but inasmuch as a large share of the collections were made in a rather limited region several miles west of the camp, a few words concerning it may well be added. The area exhibits a transition from a hardwood forest of beech

* Papers from the Department of Botany of the University of Michigan, No. 383, and from the University Herbarium.

† Dr. Kauffman organized and directed the collecting expedition, and also made the final critical field studies of all doubtful collections. However, because of his sudden illness and death the material was not prepared for publication until this year (1932). I have since gone over all the collections carefully and am responsible for the list as it is published here. Some of the new species had been collected by Dr. Kauffman previous to this expedition, whereas others were collected for the first time at Rock River; several of these were not designated as new species at the time.

I wish to express my deep appreciation to Professor E. B. Mains for help and advice in the preparation of this paper.

A. H. S.

and maple to a mixed forest of yellow birch and hemlock. A low ledge, originating in a rough granite outcrop and extending westward for several miles, forms an approximate boundary between the two types of forest. The eastern part had been cut over many years ago; at present it is covered by a dense stand of second-growth maple. The timber on the western part had not been cut, and here we found the typical moss-covered forest floor. Under the second-growth cover at the eastern end of the ledge we found many log piles in various stages of decay. These furnished an ideal place for the development of wood-inhabiting agarics. The rich humus everywhere yielded an abundance of terrestrial forms.

We began work on September 6, 1929, and continued through September 26, when duties at the University made our return necessary. During this time, however, abundant rains and comparatively warm weather favored the development of agarics, and a large number of collections, nearly all in excellent condition, were made. All were studied carefully, but particular attention was given to the genus Mycena, twenty-four species of which were recorded, and also to the Cortinarii, with thirty-seven species recorded. Most of the latter fall in the less-known subgenera. The complete list contains two hundred and forty-five species distributed among thirty-seven genera. Critical notes are included on forty little-known species as well as complete descriptions of twenty which are presented as new. Twenty-seven other species are reported for the first time as occurring within the state; of these there are two whose presence in this country has been disputed. Since there were practically no duplicates for distribution to other herbaria, the collection numbers of the specimens have not been considered useful for publication and are cited only for new species. All the material is preserved in the herbarium of the University of Michigan.

LIST OF SPECIES

Amanita flavoconia Atk. — Growing singly in swampy places and on sandy soil under hemlock and birch.

Amanita mappa Fr. — Under hemlock.

Amanita tomentella Kromb. — Solitary under hemlock, birch, and balsam.

Amanita verna Fr. — Scattered under white birch and aspen on sandy soil. The spores were perfectly spherical, 9–12 μ.

Amanita virosa Fr. — Scattered in mixed woods of birch, hemlock, and balsam.

Amanitopsis vaginata Fr. — Common.

Armillaria granulosa (Fr.) Kauff. — Gregarious on sand under aspens.

Armillaria granosa (Morg.) Kauff. — Gregarious on rotten hardwood logs.

Armillaria mellea Fr. — Very common.

Cantharellus aurantiacus Fr. — Gregarious on an old conifer log.

Cantharellus cibarius Fr. — Gregarious on humus.

Cantharellus infundibuliformis Fr. — Frequent in low places.

Cantharellus umbonatus Fr. — Growing attached to mosses.

Claudopus nidulans Fr. — On aspen logs. The odor was still persistent in the dried specimens two years after they had been collected (15).

Clitocybe albidula Pk. — On humus in a dense birch and hemlock forest.

Clitocybe candicans Fr. — On needles under pines.

Clitocybe cartilaginea (Bull.) Bres. — Cespitose on humus under aspen.

Clitocybe cartilaginea var. **glabra** Kauffman & Smith, var. nov. — Non caespitosa; stipes glaber; sporae globosae, 3–4 μ. — Specimen typicum in Herb. Mich. conservatum, Kauffman & Smith n. 59, prope Rock River, Michigan, September 14, 1929.

Pileus 8–10 cm. broad, convex-expanded, somewhat wavy irregular, in age slightly depressed in the center, watery brown (between "wood brown" and "Isabella color," but with no tints of violaceous or olive),[1] glabrous and even, rigid, brittle from the subcartilaginous surface, moist; flesh

[1] All color names within quotation marks are taken from Ridgway, R., *Color Standards and Nomenclature.*

watery whitish, thick on the disk, rapidly thinner to the thin inflexed margin; lamellae narrowed behind and subsinuate with a decurrent tooth or line, 4–7 mm. broad, crowded or nearly so, "ivory yellow" with a gray tint near the margin of the pileus, edge entire; stipe stout, 6–10 cm. long, 2–3 cm. thick, subequal to almost clavate, whitish, glabrous, naked at apex, even, concolor within and spongy, cortex rigid, fibrous, tough; odor none, taste slightly disagreeable; spores 3–4 μ, globose or subglobose, hyaline. Growing singly under aspen and white birch. The habit, glabrous stipe, and smaller spores distinguish the variety from the species.

Clitocybe cerussata Fr. — Gregarious on humus under hardwoods.

Clitocybe clavipes Fr. — Scattered to gregarious on humus under hardwoods.

Clitocybe cyathiformis Fr. f. americana Kauff. — On an old beech log.

Clitocybe decora Fr. — Solitary on coniferous wood.

Clitocybe ectypoides Pk. — Gregarious on rotton hemlock logs.

Clitocybe infundibuliformis Fr. — Scattered to gregarious on humus under hardwoods.

Clitocybe (Laccaria) amethystina Bolt. — Scattered on humus under hemlock.

Clitocybe (Laccaria) laccata Fr. — Very common on humus.

Clitocybe (Laccaria) laccata var. striatula Pk. — Common in low moist places.

Clitocybe odora Fr. var. anisearia Pk. — Scattered on humus under hardwoods.

Clitocybe piceina Pk. — Closely gregarious on humus under hemlock.

Clitocybe regularis Pk. — Scattered on pine needles.

Clitopilus abortivus B. & C. — Gregarious at the base of a cherry stub in an open wood of maple and cherry.

Collybia acervata Fr. — Cespitose to densely gregarious on humus and débris in mixed woods.

Collybia albiflavida (Pk.) Kauff. — Solitary on humus under aspens.

Collybia butyracea Fr. — Common.

Collybia cirrata Fr. — On old fungous remains.

Collybia familia Pk. — Cespitose on coniferous logs.

Collybia hariolorum Fr. var. **inodora** Kauffman & Smith, var. nov. — Inodora; stipes firmus, fere glaber; sporae 5–6 × 2.5–3 μ. Specimen typicum in Herb. Mich. conservatum, Kauffman & Smith n. 156, prope Rock River, Michigan, September 16, 1929.

Pileus 2–3.5 cm. broad, flattened or slightly convex, rather soft and flexible, glabrous, even, "ochraceous-tawny" to "ochraceous-buff," margin very thin and sometimes faintly short-striatulate, at length narrowly upturned; flesh white, rather thin; lamellae narrowly adnexed, narrow, crowded, pure white when fresh, creamy in age, edge entire; stipe short, 2–3 cm. × 2–4 (5) mm., terete or compressed, hollow, concolor, appearing almost glabrous but clothed throughout by microscopic spreading hairs, even, base slightly enlarged and intergrown with débris, usually with a few very slender white rhizomorphs; odor slight; taste mild to slowly subnauseous or bitter; spores subfusiform, 5–6 × 2.5–3 μ; cystidia none; sterile cells not differentiated; basidia 20 × 4–5 μ, 4-spored; gill-trama parallel. These plants differed from typical material in the lack of an odor when crushed, in the stipe being firm and only minutely pubescent, and in the shorter spores. Type specimen Kauffman and Smith, No. 156.

Collybia maculata A. & S. — Under aspens.

Collybia plexipes Fr. (*sensu* Kauffman, *The Agaricaceae of Michigan*). — On hardwood.

Collybia radicata Fr. — A single large plant was found with a pileus 15 cm. broad and a stipe 25 cm. long.

Coprinus atramentarius Fr. — In frondose woods.

Cortinarius acutus Fr. — On mossy soil in mixed woods. The outstanding characteristics of these specimens were the conical pilei, which became repand in age, their chamois color and prominent striations, the hyaline yellowish or pallid

stipe, and the distant lamellae. The typical Friesian species has close lamellae, but this single variation is not sufficient to justify a separation.

Cortinarius albidoavellaneus Kauffman & Smith, sp. nov. (Pl. XXIII). — Inodorus et insaporus; pileus 4–6.5 cm. latus, carnosus, campanulatus, obtusus, hygrophanus, glaber, subviscidus, pallido-avellaneus, non pelliculosus; velum universale exiguum; lamellae adnatae, confertae, pallidae demum cinnamomeae; stipes 8–12 cm. longus, 5–9 mm. crassus, solidus, pallidus, aequaliter cylindricus vel basi incrassatus, exigue fibrillosus, apice glaber; sporae subglobosae, tuberculosae, 7.5–8 (9) μ, basidia 50 × 8–9 μ. — Specimen typicum in Herb. Mich. conservatum, Kauffman & Smith n. 60, prope Rock River, Michigan, September 11, 1929.

Pileus 4–6.5 cm. broad, broadly subconic to campanulate, apex very obtuse or subtruncate, hygrophanous, pale tan to "clay color" except for a broad zone on the margin, which is "pinkish buff" after losing moisture, at length subexpanded, even, dry, glabrous, subviscid when moist but without a true pellicle, flexible at first or fragile, with the scanty remains of a universal veil along the margin; flesh watery whitish, then pallid, thin except on the center; lamellae ascending at first, adnate, seceding, 5 6 mm. broad, crowded, at first white or pallid, then "pinkish cinnamon," edge entire; stipe long, 8–12 cm. × 5 9 mm. below, slightly tapering, whitish, then pallid-white, silky-shining, nearly glabrous, with scanty signs of very thin appressed remnants of a universal veil, apex white furfuraceous or mealy, with short lines as of decurrent gills, solid, cortex becoming cartilaginous, concolor or watery within, stuffed; odor slight or radishy when fresh; taste mild to subnauseous; spores globose to subglobose, 7.5–8 (9) μ, dark rusty umber, obscurely or minutely tuberculate; basidia 50 × 8–9 μ, 4-spored or a few 2-spored. Found growing closely gregarious in a wet grassy place in a cedar swamp. Type specimens Kauffman and Smith, No. 60.

The position of this species in relation to other species of the genus is rather uncertain. The presence of a universal

veil and hygrophanous flesh should place it in Telamonia, but the plants which it seems to resemble most in other characteristics are in the subgenera Dermocybe and Phlegmacium. *C. ochroleucus* Fr. and its varieties are not hygrophanous, and the spores are reported as 8 × 4–5 μ. *C. albidifolius* Pk. has yellowish floccose scales on the stipe, non-hygrophanous flesh, tawny-ochraceous pilei, and slightly smaller spores. The pilei of the plants described as a variety of *C. albidifolius* in *The Agaricaceae of Michigan* possessed a definite pellicle, which was lacking in our specimens.

Cortinarius alboviolaceus Fr. — On humus under conifers.

Cortinarius anomalus Fr. — On humus in mixed woods of birch and spruce, but most abundant in low places and along the edges of bogs on the drier ground.

Cortinarius armillatus Fr. — Very common under aspens, birch, and spruce, especially along the edges of bogs.

Cortinarius brunneofulvus Fr. — Under spruce and other trees. Spores variable, 9–11 × 6–7 μ, pileus "Natal brown" to "Rood's brown" when fresh or moist, when drying the margin changes to "fawn color," and the umbo becomes "ferruginous" to "ochraceous-salmon," spore print rusty-orange; lamellae pallid-cinnamon when young, "Sayal brown" in age.

Cortinarius bulbosus Fr. (Pl. XXIV). — This is a rather large plant with a fleshy pileus, at first oval to subhemispherical, then campanulate-expanded, broadly subumbonate, obtuse, 5–8 cm. broad, surface even, covered by a thin, webby, appressed, superficial, white silkiness, "light ochraceous-salmon," "apricot orange" or "ochraceous-salmon," more or less variegated with "wood brown," especially on the umbo or disk, margin at first involute, at length broadly decurved, thin and whitened by the veil; context compact on the disk, brittle in age, concolor when moist, soon whitish; odor and taste earthy, scarcely subnauseous; lamellae adnate, sometimes emarginate or with a decurrent tooth, rather close, distinct, varying from narrow to quite broad in large plants, at very first "light ochraceous-buff," soon "tawny" or darker

in age, never with violaceous tints, edge entire; stipe clavate-bulbous, solid, tapering upward, paler than pileus, at first covered by a white, silky universal veil which is sometimes subperonate or interwoven, at length sordid and superficially fibrillose-silky, corticated, concolor within, 5–7 cm. long, 10–18 (26) mm. thick above the large bulb; spores short-ellipsoid, scarcely rough, 7–8 (9) × 4–5 (6) μ. On the ground under aspen and balsam. Distribution for the United States: New York, September 21, 1921, C. H. Kauffman; Oregon, October 10, 1922; Michigan, September 11, 1929.

A smaller form also occurs (not found at Rock River), which has a pileus 1.5–6 cm. broad, obtusely oval to sub-campanulate, then broadly campanulate with an obtuse umbo, or expanded and plane, hygrophanous, russet to "ochraceous-tawny" when young and moist, dingy "cinnamon-rufous" or "hazel" when dry, variegated at first by innate white fibrils but glabrous and sordid in age, even, margin at first incurved and white silky from the cortina; flesh concolor when moist, dingy whitish when dry, thick on the disk, abruptly thinner halfway to margin; lamellae adnate to emarginate, medium close to subdistant, 8 mm. broad, ventricose in age, pallid, at first subavellaneous, finally "tawny" or "cinnamon-brown," thickish, edge entire; stipe white, and usually broadly zoned at the middle or just above the bulb, solid at first, 2–3 cm. long, 6–15 mm. thick, variable in thickness from equal to clavate-bulbous with a short pointed base; spores 6–7 × 3–4 μ. The generally smaller size and more cylindric stipe are its outstanding characteristics, but there is a great deal of intergradation.

Cortinarius castaneus Fr. — On a mossy hummock under birch and aspen.

Cortinarius cinnamomeus Fr. — On sphagnum and under hemlock on high ground.

Cortinarius clandestinus Kauffman, 8*a*, 348 (Pl. XXV).—Pileus 3–6 cm. latus, subcarnosus, campanulato-convexus, obsolete umbonatus, ochraceo-cinnamomeus, siccus, villoso-squamulosus; cortina olivaceo-flava; lamellae adnatae vel sinuatae,

angustae, confertae, pallidae demum fulvae; stipes 6–10 cm. longus, 5–10 mm. crassus, cylindricus, farctus, infra fibrillosum annulum exigue fibrillosus; sporae subglobosae vel late ellipsoidales, leves, 6–7 × 5–6 μ. — Specimen typicum in Herb. Mich. conservatum, Kauffman, prope Lake Cushman, Olympic Mountains, Washington, October 19, 1915. Distributio: Washington, Idaho, Oregon, Michigan.

Pileus 3–6 cm. broad, slightly fleshy, campanulate-convex, then plane, at first umbonate, at length depressed around the vanishing umbo, surface dry, at first covered by dense, minute, "clove brown" fibrillose scales, later the "old gold" ground color appears on the margin of the pileus and between the scales, disk at length darker; margin thin, at first incurved, then spreading and soon split, sometimes decorated at first by the olivaceous or yellowish silky cortina; context thin except on disk, rather fragile, yellowish olivaceous, darker at first, odor distinctly of radish or sometimes slight; lamellae adnate, then sinuate, usually rather narrow, close, at very first pallid, soon lutescent or with olivaceous tinge, finally "raw Sienna," edge minutely white-flocculose; stipe equal or slightly enlarged below, stuffed then hollow, obsoletely peronate by a "light green-yellow" universal veil, but usually merely fibrillose up to the obscure annular zone or glabrescent, sublutescent within, 6–10 cm. long, 5–10 mm. thick; spores broadly elliptical to subglobose, smooth under high magnification, 6–7 × 5–6 μ, dark rusty brown under microscope. Type specimen Kauffman. Distribution: Washington, October 19, 1915; Idaho, September 11, 1922; Oregon, October 10, 1922; Michigan, September 13, 1929.

This species differs from *C. raphanoides* Fr. in the subglobose spores and the lack of an acrid taste; from *C. lutescens* in the lack of yellow colors and longer stipe; and from *C. depexus* by the greenish universal veil.

Cortinarius confusus Kauffman & Smith, sp. nov. (Pl. XXVI). — Pileus 2 5 cm. latus, carnosus, obtuse campanulatus, subhygrophanus, glaber, testaceus; cortina crocea; lamellae adnatae, flavae, demum cinnamomeae, 6–8 mm. latae, con-

fertae; stipes 7–10 cm. longus, 7–10 mm. crassus, cylindricus, fulvus, apice paene glaber; annulus evanescenter fibrillosus; sporae tuberculosae, late ellipsoideae vel ovoideae, 7–8 × 5–6 μ. — Specimen typicum in Herb. Mich. conservatum, Kauffman & Smith n. 137, prope Rock River, Michigan, September 22, 1929.

Pileus (2) 3–5 cm. broad, fleshy, pliant, obtuse, subumbonate to broadly campanulate, somewhat hygrophanous, glabrous, when young "ochraceous-tawny" to "ochraceous-orange" with a "buff-yellow" cortina and a "buff-yellow" universal veil which is quickly evanescent on the pileus; flesh concolor, fading to pale yellowish white, 3–5 mm. thick near the stipe, tapering to the margin; lamellae broadly adnate, then subemarginate, at first pale watery yellow, then "yellow ocher," finally darker at maturity, broad (6–8 mm.), close, scarcely subdistant, edge concolor and entire; stipe 7–10 cm. × 7–10 mm., cylindrical, abruptly attenuate by a short subrooting base, covered by a dense fibrillose "antimony yellow" or "tawny" sheath which partly disappears in age and which terminates in a superior fibrillose evanescent annulus, silky to nearly glabrous above, when young "maize yellow," soon fulvescent, stuffed with a soft fibrous pith, cortex rigid-elastic, odor slight or none; taste mild; spores 7–8 × 5–6 μ, rusty yellow, minutely tuberculate. Closely gregarious on sphagnum in a cedar swamp. Type specimen Kauffman and Smith, No. 137.

This species is related to *C. gentilis* in Telamonia and to *C. Whitii* in Inoloma. It differs from the former in the close lamellae, colors, and lack of an acute umbo; from the latter, in the fibrillose sheath on the stipe and in the spore size.

Cortinarius deceptivus Kauff. — On humus and moss under spruce and hemlock.

Cortinarius emollitus Fr. *sensu* Ricken (26) (Pl. XXVII). — Since this plant has not been previously recognized in this country a description seems advisable. Pileus 3–7 cm. broad, campanulate or with a broad rather obtuse umbo when partly

expanded, viscid but soon becoming dry and very shiny, somewhat hygrophanous, glabrous, "wood brown" to "avellaneous," the umbo tinged with brown or "pinkish cinnamon" to "pinkish buff" when losing moisture; margin thin and narrowly white silky; flesh concolor, very thin on the margin, thick on the disk; lamellae rather broad behind and broadly adnate, tapering to a point in front, close to almost subdistant, pallid at first then pale "cinnamon," edge minutely crenulate-erose; stipe clavate below with a short obtuse point, terete or subcompressed, whitish within, white-cortinate on the surface, fibrils at length dingy, even, glabrescent, soft but solid within; taste slowly bitterish; odor somewhat noticeable, somewhat radishy; spores 7–8.5 × 4–5 μ, nearly smooth. Habitat: Under spruce, on humus and débris. The dull colors and lack of a gelatinizing universal veil distinguish this species from *C. causticum* Fr.

Cortinarius erythrinus Fr. — On humus under frondose trees. When wet the pileus is very shiny as if viscid, the umbo is black or "bone brown," the margin is "vinaceous-fawn" or "vinaceous-buff," surface innately silky and even. The apex of the stipe has a violet sheen, but is colored like the cap within. The cortina is tinted violaceous white, but is very evanescent.

Cortinarius evernius Fr. — On sphagnum under cedar.

Cortinarius flexipes Fr. var. minor Kauff. — On humus in a cedar swamp.

Cortinarius fuscoviolaceus Pk. — Pileus conic-campanulate, 1–2 cm. broad, "chestnut" to "Mars brown" when moist, "ochraceous-tawny" when faded, lamellae scarcely subdistant, rather broad, stipe dark violet, pallid in age, sometimes with a median white cortinate annulus.

Cortinarius hemitrichus Fr. — On moss in spruce and balsam bog.

Cortinarius Kauffmanianus A. H. Smith, sp. nov. — Pileus 2–3.5 cm. latus, obtuso-umbonatus vel expansus, lentus, hygrophanus, fuscus vel rufus, glaber; cortina albida vel subviolacea; lamellae adnatae vel emarginatae, latae, pallido-

caesiae demum cinnamomeae; stipes 3–4 cm. longus, 4–7 mm. crassus, violaceus, albido-fibrillosus; sporae ellipsoideae, fere leves, 6–7.5 × 3–4 μ. — Specimen typicum in Herb. Mich. conservatum, Kauffman & Smith n. 16, prope Rock River, Michigan, September 8, 1929.

Pileus 2–3.5 cm. broad, at first obtuse, rounded or semi-ovate, later expanded and with a broad obtuse umbo, rather tough and splitting radially, hygrophanous, at first "mummy brown," then "bister" or "drab" fading to "hazel" on the umbo, which develops a definite reddish tint in age, "salmon-buff" toward the margin, glabrous, lubricous when fresh and moist; margin even and incurved at first; cortina white or violaceous-tinted; flesh of pileus thin and firm at first, concolor; lamellae adnate, becoming emarginate, rather broad, thin, easily flattening, at first pale caesius, intermediate stage violaceous, finally drab-brownish, edge minutely but unevenly serrulate; stipe 3–4 cm. × 4–7 mm. thick, violaceous under the white-silky surface; odor and taste slightly soapy; spores 6–7.5 × 3–4 μ, elliptical, almost smooth, obtuse. Type collected under spruce and cedar in a sphagnum bog, September 8, 1929, Kauffman and Smith, No. 16.

Since Ricken has interpreted a similar plant, with spores 9–12 × 6–7 μ, as the *Cortinarius cypriacus* of Fries, it seems best to describe this as a new species.

Cortinarius impolitus Kauff. — On a bare sandy hillside, under aspen and birch.

Cortinarius malicorius Fr. — On humus under hemlock and spruce.

Cortinarius montanus Kauffman, 8*a*, 348 (Pl.XXVIII). — Pileus 5–10 cm. latus, carnosus, iuventute convexus demum expansus, glaber, viscosus, castaneus; lamellae adnato-emarginatae, angustae, pallido-flavae demum olivaceo-castaneae vel olivaceo-purpurascentes; stipes farctus demum cavus, firmus, violaceus, albido-fibrillosus, basi bulbosus superne profunde concavus; velum universale flavum; sporae subamygdaloideae, tuberculosae, 9–11 (12) × 5–6 μ. — Specimen typicum in Herb. Mich. conservatum, Kauffman, prope Lake

Cushman, Washington, October 2, 1915. Distributio: Washington, Oregon, Michigan, New York.

Pileus 5–10 cm. broad, fleshy, broadly convex to subhemispherical at first, then expanded and discoid with a decurved margin, surface viscid from the thick adnate pellicle, glutinous when wet, at first variegated "hazel" or "Dresden brown" with "light yellowish olive" margin, becoming "tawny," "ochraceous-tawny," or "clay color," umber on the disk, even, glabrous; context up to 15 mm. thick, rather compact, abruptly thin on the margin, whitish or with a tinge of the color of the pileus; odor and taste mild; lamellae emarginate-adnexed, at first adnate, rather narrow (5–7 mm.), close, at first "light yellowish olive" or olivaceous, at length "buffy olive" to "Prout's brown," edge entire; stipe firm, delicately white silky fibrillose, stuffed by a white fibrous pith, then hollow, surface at first "pale Windsor blue" to "pearl blue," concolor within, equal above the prominent emarginate-depressed oblique bulb, which is at first covered by the "light chalcedony yellow" universal veil, soon sordid, becoming soft-spongy, 4 7 cm. long, 10–25 mm. thick, bulb much thicker; spores ellipsoid to slightly almond-shaped, tuberculate, light rusty brown, 9–11 (12) × 5.5–6.5 (7) μ. Type collected on humus in dense coniferous forest of cedar and hemlock, Lake Cushman, Washington, October 2, 1915. Distribution: Washington; Oregon, October 3, 1922; Idaho, August 3, 1922; New York, September 8, 1914; Michigan, 1929.

This species differs from *C. herpeticus* in its larger spores and the more brownish shades of the cap; from *C. scaurus* in the yellowish universal veil, thicker flesh, generally larger stature, and lack of any spots on the cap. Bresadola describes and figures a plant under the name *C. scaurus* Fr., which lacks the spots on the pileus and which, save for the fact that no mention is made of a universal veil, might easily be our species.

Cortinarius mucifluus Fr. — On humus. Common in mixed spruce, hemlock, birch, and aspen woods.

Cortinarius multiformis Fr. — A single collection was made which varied considerably from what is considered typical. A description follows: Pileus 4–8 cm. broad, firm and fleshy, broadly convex and obtuse at first, then expanded-plane, viscid, even, glabrous, or minutely areolate-scaly from the drying gluten, "clay color" to "ochraceous-orange," when fresh and unexpanded, becoming "warm buff" with a "tawny" disk; flesh white, thick on the disk, abruptly thin on the margin; lamellae whitish at first, soon "cinnamon-buff," narrow, arcuate at first, finally ascending, crowded, edge minutely flocculose-crenulate; stipe 5–9 cm. × 1–2 cm., often rather stout, subbulbous, bulb neither marginate nor abruptly bulbous, solid, white at first beneath the chamois-colored or "Naples yellow" remnants of the universal veil, white within, firm, bulb white-mycelioid; odor slight; taste slowly subnauseous; cortina white, not abundant; spores 8–9 × 4.5–5.5 μ, elliptical, slightly rough. Habitat: On rocky soil under spruce near a swamp. No sign of an abrupt bulb was present on even the youngest specimens of this collection, but the plants certainly belong here.

Cortinarius obtusus Fr. — On mossy places in mixed woods. Pileus "russet" on the disk to "tawny" on the margin, stipe "tawny."

Cortinarius olivaceofulvus Kauffman & Smith, sp. nov. — Pileus 5–12 mm. latus, subcarnosus, conico-campanulatus, fibrilloso-squamulosus, olivaceus demum fulvus; lamellae adnatae, distantes, latae, olivaceae demum olivaceo-cinnamomeae; stipes 2–4 cm. longus, 1–1.5 mm. crassus, cylindricus, glaber, ochraceo-olivaceus, firmus; sporae ellipsoideae, tuberculosae, 7–8 × 3.5–4.5 μ. — Specimen typicum in Herb. Mich. conservatum, Kauffman & Smith n. 42, prope Rock River, Michigan, September 10, 1929.

Pileus small, 5–12 mm. broad when mature, subfleshy, at first conical, then persistently subconic-campanulate, not expanded, at length with an obtusely conical umbo, covered at first by conspicuous appressed fibrils, then minutely scaly, in age glabrescent or silky, "tawny-olive" fading

slowly to "clay color" or "cinnamon-buff" at times, margin at first connivent, soon turned inward, with a few evanescent minute remnants of a veil in age; flesh concolor, slightly moist and changing slowly, not truly hygrophanous but at length pallid; lamellae obtusely adnate, distant, rather broad, at first "tawny-olive," at length "sepia," edge entire; stipe 2–4 cm. long, 1–1.5 mm. thick, equal, glabrous, innately silky and shining, pale tawny olive, even, hollow, concolor within, subrigid, strict, flexuous; cortina scanty, concolor, soon evanescent; odor none; taste mild; spores 7–8 × 3.5–4.5 μ, short ellipsoid, dark rusty brown, smooth or nearly so. Type collected under aspen and birch on humus, September 10, 1929, Kauffman and Smith, No. 42. This species differs from *C. raphanoides* in the lack of odor, mild taste, stature, slightly smaller spores, duller colors, and distant lamellae. From *C. clandestinus* it differs in the much smaller size, the shape of the pileus, and ellipsoid spores.

Cortinarius paleaceus Fr. — On wet muck under maple. Pileus, stipe, and flesh were "Quaker drab" at first, but the pileus became darker, assuming fuscous tints.

Cortinarius pholideus Fr. — On very rotten wood, débris under aspens, and in sphagnum bogs where it was attached to débris beneath the moss.

Cortinarius punctatus Fr. — On humus in a mixed forest. This species differs from *C. badius* in the solid stipe, changing colors, and larger size.

Cortinarius rigidus Fr. — On sphagnum under cedars.

Cortinarius rimosus Pk. (Pl. XXIX). — Under poplar and white birch in sandy soil. The spores of plants in this collection measured 8–10 × 5–6 μ. The rimose character was very marked on the pileus, but the lamellae were scarcely subdistant. The pileus and stipe are provided with a rather rigid cortex which cracks, especially after rains, giving the characteristic appearance. The odor and taste were not distinctive.

Cortinarius semisanguineus (Fr.) Kauff. — On sphagnum.

Cortinarius splendidus Pk. — Under hemlock and balsam near the edge of a bog.

Cortinarius subobtusus Kauffman & Smith, sp. nov. — Pileus 1–2.5 cm. latus, firmus, campanulato-convexus, obtusus, sericeus demum glaber, ferrugineus, hygrophanus; lamellae pallide cinnamomeae, demum fulvae, latae, confertae vel subdistantes, adnatae abrupte et brevissime decurrentes; stipes 2–3 cm. longus, 3–4 mm. crassus, cylindricus, subfirmus, cavus, albo-sericeo-fibrillosus, castaneus; sporae ellipsoideae, tuberculosae, 6–7.5 × 3.5–4.5 μ. — Specimen typicum in Herb. Mich. conservatum, Kauffman & Smith n. 63, prope Rock River, Michigan, September 11, 1929.

Pileus 1–2.5 cm. broad, rather firm and subrigid, at first oval with the margin connivent, becoming campanulate-convex, very obtuse or obtusely umbonate, expanded, very finely silky at first, then glabrous and even, radiately wrinkled when drying, "Prout's brown" when young, becoming "cinnamon-brown," fading to "ferruginous" on the umbo and "light ochraceous-buff" elsewhere; flesh concolor, thin, hygrophanous; lamellae at first pallid cinnamon, at length "ochraceous-tawny," rather broad, almost subdistant or close, adnate with a decurrent tooth, edge entire; stipe short, equal, hollow, subrigid, 2–3 cm. long, relatively stout, (2) 3–4 mm. thick, "Prout's brown" within and without, white silky from the cortina, zoned at about or below the middle from remnants of the cortina; odor none; taste slightly or tardily subnauseous; spores 6–7.5 × 3.5–4.5 μ, short ellipsoid, minutely rough, pallid ochraceous brown under the microscope. Type collected September 11, 1929, growing gregariously under spruce on rocky soil covered by a carpet of moss. Kauffman and Smith, No. 63. This species resembles *C. erythrinus* in stature, but not in color. *C. leucopus* is a larger plant with a conical cap, which is acutely umbonate in age. The dark brown stipe, which is thick in comparison with the width of the pileus, the obtuse umbo, and the squatty appearance distinguish this species.

Cortinarius uraceus Fr. — Under cedars in humus and débris. The spores of these plants measured 7–9 × 5–6.6 μ.

Cortinarius vibratilis Fr. — On moss under conifers. This was the typical or small form.

Crepidotus crocophyllus Berk. — On a yellow birch log.

Crepidotus versutus Pk. — On decaying aspen logs.

Entoloma grayanum Pk. — On humus in mixed woods.

Entoloma griseum Pk. — On very rotten logs.

Entoloma lividum Fr. — On humus in mixed woods.

Entoloma speculum Fr. — Under hemlock.

Entoloma strictius Pk. — On the edge of a sphagnum bog under spruce.

Flammula flavidella Murr. — On hardwood logs.

Flammula gummosa Fr. — On humus under birch.

Flammula penetrans Fr. — On cedar and spruce logs.

Flammula polychroa Berk. — On hemlock logs.

Flammula spumosa Fr. — On the ground and débris; also birch logs.

Galera hypnorum Fr. — On a very old moss-covered hemlock log in a dense forest.

Galera procera Atk. — On humus in an old logging road through a birch-maple area.

Galera sphagnorum Fr. — On sphagnum.

Galera subhypnorum Atk. — On moss and débris in frondose woods.

Gomphidius flavipes Pk. — Pileus 3–4 cm. broad, convex, expanded and repand in age, obtuse or subumbonate, even, viscid, viscidity soon slight, pellicle thin, minutely tomentose on the disk from the drying gluten and with silky fibrils on the margin, "vinaceous-pink" when fresh, becoming duller in age; lamellae "pale pinkish buff," distant, arcuate, subdecurrent, very few forked, thick, at length sprinkled by the spores, 4–5 mm. broad midway between margin and stipe, often transversely wrinkled, edge entire; stipe 5–8 cm. long, equal above, tapering below to a pointed base, white above, "picric yellow" or brighter below both inside and out, solid, becoming soft, silky or lacerate-silky at the apex, slightly fibrillose downward, sometimes curved or twisted; odor none; taste mild; spores 20–25 (30) × 6–7.5 μ, narrowly

clavate, obtuse; cystidia cylindrical, tapering at the base, abundant, up to 140 μ long, 11–15 μ wide. Habitat: Under *Alnus incana* in a sphagnum bog. The bright yellow base serves to distinguish this species from *G. superiorensis* macroscopically. The difference in spore size is the most reliable microscopic characteristic.

Gomphidius superiorensis Kauffman & Smith, sp. nov. (Pl. XXX). — Pileus 1.5–4.5 cm. latus, conico-campanulatus vel papillatus, viscidus, levis, glaber, ochraceus; margine deflexus; lamellae arcuatae, confertae vel subdistantes, interdum furcatae, crassae; stipes solidus, 4–9 cm. longus, 5–14 mm. crassus, basi attenuatus, ochraceus, non croceus; sporae subfusiformes, 14–19 × 6–6.5 μ; cystidia cylindrica, 98–112 × 10–14 μ. — Specimen typicum in Herb. Mich. conservatum, Kauffman & Smith n. 92, prope Rock River, Michigan, September 14, 1929.

Pileus 1.5–4.5 cm. broad, at first papillate and hemispherical or at times subconic or campanulate, becoming broadly campanulate-expanded with a decurved margin and a small but conspicuous papillate umbo, at length turbinate, surface viscid, gelatinous in wet weather, even, glabrous, "Natal brown" to "army brown," tinged "ochraceous-buff" where the pellicle has been removed, at times deeply diffracted-scaly in age from drying; flesh of pileus "ochraceous-buff" becoming dingy, thin on the margin, thick in the center; lamellae at first arcuate, broad, at length inversely ascending, close, almost subdistant, only a few forked near the stipe, "cinnamon-buff" at first, soon "clay color" to "tawny-olive," at length sprinkled by black spores, edge entire, concolor; stipe solid, varying in length and thickness, normally 4–6 cm. long, frequently 7–9 cm. long, 5–6 mm. thick, at times 7–14 mm. thick, tapering downward at the base, subequal or equal upwards, "ochraceous-buff" inside and out, sometimes with a faint salmon tint but never truly yellow at the base, base sordid and obtusely pointed, even, fibrillose downward, or glabrescent with scattered fibrils; cortina "ochraceous-buff," more or less scanty, but frequently

leaving fibrillose remnants on the stipe; taste slight or mild, odor none; spores 14–19 × 6–6.5 μ, elongated, elliptically subfusiform, obtuse at ends, smoky-colored under the microscope; cystidia 98–112 × 10–14 μ, cylindrical, obtuse, tapering to a pedicel at the base, scattered to numerous. Habitat: Growing scattered in sphagnum under bushes around the edge of a bog. Type collected September 14, 1929, near Rock River, Kauffman and Smith, No. 92.

Gomphidius viscidus Fr. — Pileus "pecan brown" to "vinaceous-tawny"; stipe "deep chrome," soon "ochraceous-buff"; spores 15–20 × 5–6 μ; solitary in low moist woods of conifer and white birch.

Hebeloma avellaneum Kauffman, sp. nov. — Caespitosum vel subcaespitosum; pileus 3–8 cm. latus, ovato-campanulatus, umbonatus demum expansus, avellaneus, valde viscosus; lamellae adnato-emarginatae vel adnatae, brevissime et angulatim decurrentes, angustae, confertae, avellaneae, acie albido-fimbriatae, non guttulatae; stipes 5–10 cm. longus, 6–12 mm. crassus, ovoideo-bulbosus, farctus, demum cavus, albido-furfuraceus, basi sericeus; sporae amygdaloideae, tuberculosae, 8–10 (11) × 5–5.5 μ. — Specimen typicum in Herb. Mich. conservatum, C. H. Kauffman, prope Lake Quiniault, Washington, November 8, 1925. Distributio: Washington, Idaho, Michigan.

Pileus 3–9 cm. broad, oval to ovate-campanulate, soon broadly umbonate, then expanded, the umbo disappearing, "orange-cinnamon" or "wood brown" to "avellaneous," "fawn color" or "cinnamon-buff" on the disk, "pinkish buff" on the margin and becoming dingy "ochraceous-buff" to "ochraceous-tawny" in age, very viscid, shining glabrous, margin whitish; lamellae adnate, often emarginate with a decurrent tooth in age, narrow, crowded, narrowed to a point in front, "vinaceous-buff" then "avellaneous" with a tinge of cinnamon in age, edge white flocculose, not beaded; stipe 5–10 cm. × 6–12 mm., elongated, ovate-bulbous, solid at first, stuffed, then narrowly hollow, somewhat corticate to fibrous, covered by a removable floccose or scurfy white

mealiness, especially at the apex, silky-glabrescent below, white within; mycelium white; odor none, taste mild or bitter; spores 8–10 (11) × 5–5.5 μ, somewhat almond-shaped, slightly roughened, pale brown; basidia 4-spored, 32 × 6–7 μ; sterile cells long, 60–80 × 5–8 μ, abundant; cystidia none. Cespitose to subcespitose on humus under conifers and along the borders of swamps. Type collected at Lake Quiniault, Washington, November 8, 1925, by C. H. Kauffman. Distribution: Washington; Idaho, September 13, 1922; Michigan. This species is near *H. punctatum* and *H. versipelle,* but the former is smaller with shorter sterile cells, whereas the latter has broad lamellae and larger spores.

Hebeloma fastibile Fr. — On humus among maple, beech, and hemlock.

Hebeloma parvifructum Pk. — On humus among hardwoods.

Hygrophorus auratocephalus Ellis. — Pileus 3–5 cm. broad, at first obtusely conic, then campanulate and conspicuously umbonate, "cadmium yellow," "deep chrome," or "yellow ocher" when moist, slightly hygrophanous, slightly viscid from a thin subseparable pellicle, even on the margin, young plants appearing faintly innately silky, in age the flesh splits radially on the elevated margin; flesh concolor when moist, soon fading to white, fragile, equally thin; lamellae broadly adnate, with a triangular decurrent tooth, very broad, ventricose, subdistant to distant, "Capucine yellow" to "cadmium yellow" when fresh, not golden yellow, thickish, edge concolor; stipe 4–7 cm. long, tapering gradually downward, 7 mm. thick at apex, 2–3 mm. thick at the base, moist or slightly subviscid, "mustard yellow" over all or whitish at the base, terete, strict, subfragile, hollow, very large; odor slight at first, becoming rather penetrating after a time, taste slightly disagreeable; spores 7–8 × 4–5 μ, ellipsoid, apiculate, smooth, hyaline; basidia 4-spored, 45–50 × 6–7 μ, tapering downward; cystidia none; gill-trama interwoven toward the hymenium, less so toward the axis. Growing scattered in wet places along streams or on springy ground, usually under conifers.

HYGROPHORUS BOREALIS Pk. (Pl. XXXI). — Gregarious on sphagnum, and on humus in mixed woods.

HYGROPHORUS CERACEUS Fr. — Scattered on moss in cedar and balsam swamps.

HYGROPHORUS COCCINEUS Fr. — On sphagnum. Pileus "grenadine red" to "scarlet-red"; lamellae almost whitish, tinted yellow or reddish; stipe "deep chrome," base almost white; spores 7–8 × 4–5 μ.

HYGROPHORUS CONICUS Fr. — On mossy road through frondose woods. A rather stout plant, but showing the characteristic blackening at the base. Both 2- and 4-spored basidia were found on a single pileus. The spores were all of the same size, 8–10 × 5.5–6 μ.

HYGROPHORUS DAVISII Pk. — In a cedar swamp.

HYGROPHORUS FULIGINEUS Frost & Peck (20) — Pileus 3–7 cm. broad, convex, rounded campanulate, subexpanded and umbonate, the umbo often obsolete in age, when young blackish "clove brown" with an "olive-brown" margin, in dried specimens the disk reddish brown or dark fuliginous and the margin pale fuliginous, covered by a thick layer of hyaline gluten, glabrous; lamellae white or creamy white, pale ochraceous in dried specimens, edge entire, subdistant, decurrent, medium broad; stipe white under the thick hyaline gluten, annulate from the cortina, very white and silky above the annulus; annulus evanescent, becoming fuscous, dotted below from the drying gluten; odor and taste mild; spores 7–8.5 × 5–6 μ, short-ellipsoid, obtuse, hyaline, smooth, or slightly rough under high magnifications; cystidia none; gill-trama divergent; basidia long, 48–50 × 7–8 μ, 4-spored. Under cedar, hemlock, and birch on the border of a cedar swamp. Gregarious. The hyaline glutinous universal veil, the dark, dull color of the pileus, the white flesh and gills, and the spots which develop in age on the stipe make it distinct from *H. hypothejus* Fr. The spore size, habitat, etc., do not allow it to be placed in *H. olivaceo-albus* Fr.

HYGROPHORUS MINIATUS Fr. — On humus.

HYGROPHORUS NITIDUS B. & C. — Scattered on mosses in moist mixed forest of hemlock and maple.

HYGROPHORUS NIVEUS Fr. — On a mossy log in a cedar swamp.

HYGROPHORUS PALLIDUS Pk. — Gregarious on humus and moss under cedar.

HYGROPHORUS PECKII Atk. — Gregarious on humus and moss under cedar, or on high ground in mixed forests.

HYGROPHORUS PUNICEUS Fr. — Scattered on sphagnum in a cedar swamp, also under hemlock. The stipe was pale yellow to reddish.

HYGROPHORUS RICKENII Maire. — Pileus 3 4 cm. broad, conic and obtuse at first, then campanulate-expanded with a conspicuous obtusely conic umbo, "cadmium yellow," unicolorous, viscid, glutinous in wet weather, not blackening when bruised or in aging, glabrous and even, margin thin and splitting easily; flesh soft, thin on the margin, thick on the disk; lamellae ascending, free or narrowly adnexed, ventricose, medium broad (2–4 mm.), close to subdistant, edge entire and concolor; stipe 6–8 cm. × 3–6 (7) mm., terete, compressed, or twisted striate, fibrillose to glabrous, equal or subequal, light "cadmium yellow" inside and out, paler at the base, subviscid to viscid, not blackening; odor none; taste mild; spores 9–11 × 4–5 μ, or 11–15 × 6–7 μ, oblong subtruncate, hyaline, smooth, the larger spores produced on the bispored basidia; basidia 40–45 × 8–10 μ, 2- and 4-spored on a single fruit-body; cystidia none; gill-trama parallel.

Hygrophorus obrusseus Fr. is described by Lange as having a very broad obtuse cap and 4-spored basidia. The same author describes the rather slender, conical plant with bispored basidia, which Ricken placed in *H. obrusseus*, as a new species, *H. constans*. Our plants were the slender type with conical pilei and the colors as Ricken describes them. The spores of *H. obrusseus* Fr.–Lange are given as 7.5 × 5 μ. Those of our plants fall within Ricken's range, 12–15 × 7–8 μ, and since Ricken was dealing with the bispored form it seems very probable that we have his plant and, with Kühner (16), we think that it should be separated from *H. obrusseus* Fr.–Lange. It was found growing singly on humus in a

beech-maple forest. Since the name *H. constans* is untenable, Maire (18) has changed it to *H. Rickenii.*

Hypholoma capnoides Fr. — On very decayed wood in a hemlock forest.

Hypholoma hydrophilum Fr. *sensu* Ricken. — Densely gregarious on old hardwood logs.

Hypholoma perplexum Pk. — On a birch stump.

Hypholoma sublateritium Fr. — Around an old hardwood stump.

Inocybe fastigiata (Schaeff.) Karst. — Scattered on humus under cedars.

Inocybe geophylla Fr. — Gregarious on humus in cedar swamp.

Inocybe geophylla Fr. f. perplexa Kauff. — Gregarious on humus and débris under cedar.

Inocybe pallidipes E. & E. — Scattered on grassy soil in an aspen area.

Inocybe subtomentosa Pk. — Scattered on grassy soil in an old road.

Inocybe ventricosa Atk. — Scattered on moss along an old road.

Lactarius alpinus Pk. — Gregarious on moss in swamps. Intensely acrid.

Lactarius aspideoides Burl. — Under hemlock on humus at the edge of a spruce bog. The bitter, astringent taste, along with the zonations of the pileus, place our plants here rather than in *L. aspideus* Fr.

Lactarius cilicioides Fr. — On humus under aspens.

Lactarius deceptivus Pk. — Solitary under conifers in a sphagnum bog.

Lactarius deliciosus Fr. — On moss at edge of bog.

Lactarius glabripes A. H. Smith, sp. nov. — Pileus 2–3.5 cm. latus, iuventute planus umbone parvo praeditus, demum infundibuliformis, fibrillose squamulosus; margine sericeo-fibrillosus et raro substriatus; lamellae subdecurrentes, interdum furcatae, pallido-ochraceae, confertae, angustae; stipes 2–3 cm. longus, 2–4 mm. crassus, concolor, cylindricus, glaber, cavus; lac album, immutabile, mite; sporae 7.5–10 × 6–8.5 μ. — Specimen typicum in Herb. Mich. con-

servatum, Kauffman & Smith n. 176a, prope Rock River, Michigan, September 18, 1929.

Pileus 2–3.5 cm. broad, "pinkish buff" to "cream-buff," the umbilicate-depressed center darker and with minute "Isabella color" scales, appressed silky-pubescent toward the margin, the thin membranous margin spreading, even or rarely substriate in age; flesh pallid or whitish, thin; lamellae inversely ascending, subdecurrent, a few forked or anastomosing, pale yellowish when fresh or "warm buff" varying to "cream color," distinct but close, narrow, slightly darker in age, edge entire; stipe 2–3 cm. × 2–4 (5) mm., colored like the pileus, slightly tapering upward or equal, glabrous, terete, even, hollow; milk white, unchanging and not staining the lamellae brownish, mild; odor none; spores 7.5–10 × 6–8.5 μ, broadly ellipsoid or subglobose, sparsely echinulate. Type collected by Kauffman and Smith, September 18, 1929. Growing scattered here and there in wet mossy places in mixed conifer and hardwood swamps. This plant differs from *L. luteolus* in its much smaller size, thin pileus, glabrous stipe which is dark reddish brown when dry, appressed pubescence of the cap, and mild latex which does not turn brownish when exposed to the air. From *L. subvelutinus* it differs in color, size, and glabrous stipe. It is, perhaps, closest to *L. griseus*, from which it differs in the mild latex, the pale yellowish lamellae when young, the entirely glabrous stipe, and slightly larger spores. In drying the stipe becomes a dark reddish brown which is not at all typical of *L. griseus*.

Lactarius glyciosmus Fr. — On sandy soil. Tardily acrid, odor strongly aromatic, pileus "purplish gray" on the disk, lighter elsewhere.

Lactarius helvus Fr. — Very common in sphagnum bogs.

Lactarius lignyotus Fr. — Scattered on sphagnum under cedars.

Lactarius oculatus (Pk.) Burl. — Scattered on humus under hemlock.

Lactarius pubescens Fr. — Scattered on mosses in swamps. This is the *L. vietus* of Kauffman, *The Agaricaceae of Michigan.*

Pileus "ecru-drab," pubescent, gills creamy, stipe pallid, taste slowly acrid. In one collection the lamellae turned a dark brown when wounded.

Lactarius theiogalus Fr. — On humus under hemlock and birch.

Lactarius torminosus Fr. — In mixed woods of birch and hemlock.

Lactarius trivialis var. viridilacteus Kauff. — The "cinnamon-buff" to light "ochraceous-buff" colors of the young plants distinguish this variety from the darker more smoky-colored plants found in the hardwoods of the Southern Peninsula. The greenish stains on the gills are also more pronounced.

Lactarius turpis Fr. — These plants differed from typical specimens in the zonate tendency of the pileus and its white pruinose margin when young, the lamellae not becoming ashy from the spores, and the dingy creamy-white milk.

Lactarius uvidus Fr. — Gregarious in sphagnum bogs. A small form was most common, but a few gigantic specimens were found among the smaller ones. These large plants were about 15 cm. broad. It was curious to note that no intergradations existed; the plants measured 4–8 cm. or 14–18 cm. broad.

Lactarius vietus Fr. *sensu* Bresadola. — Pileus 3.5 cm. broad, drab "olive-gray" fading to "light olive-gray," pruinose, margin cottony, viscid, depressed in the center, not striate, odor not distinctive, taste mild; lamellae white-incarnate, crowded, narrow, many-forked at the base, adnate to subdecurrent, edge even; milk white and staining the lamellae brown; stipe 5.5 cm. long, 1.5 cm. thick, tapering upward, glabrous except for the white tomentosity at the base, pallid to incarnate, flesh tint more pronounced at apex, stuffed; spores 6–7 × 5.5–6 μ, minutely echinulate; basidia 40–45 × 8–10 μ, 4-spored; cystidia awl-shaped, 90–110 × 6–9 μ. Growing singly in a beech-maple forest.

Lentinus vulpinus Fr. — Common.

Lepiota clypeolaria Fr. — Scattered on humus among second-growth maple.

Lepiota forquignoni (Quél.) Rick. — On a very decayed log in a mixed forest.

Lepiota fusispora Kauff. — On humus in mixed woods.

Leptonia asprella Fr. — Singly on sphagnum.

Marasmius androsaceus Fr. — On pine needles.

Marasmius cohaerens (Fr.) Bres. — On humus in hardwoods. Cespitose and with short stipes.

Marasmius delectans Morg. — On fallen leaves of frondose trees.

Marasmius epiphyllus Fr. — On decaying alder leaves.

Marasmius multifolius Pk. — On humus and fallen leaves in swampy woods. The pileus is "Isabella color" or "pinkish buff," then watery cinnamon when drier, odor none, gills very crowded.

Marasmius oreades Fr. — These plants were found growing in the woods and were not typical for the species, but nevertheless seem to belong here. Pileus 2–3.5 cm. broad, obtuse and flexible, rather fleshy, alutaceous, flat to convex, margin at first incurved, glabrous, not striate, even; lamellae adnexed, broad, close, whitish at first, then pale alutaceous, edge entire; stipe compressed, hollow, 3.5 cm. × 2–6 mm., furrowed, minutely velvety, whitish, or cream-buff at apex, darker elsewhere, white strigose at the base, flexible; odor none, taste disagreeable; spores 7–9 × 3 μ. The rather close lamellae, disagreeable taste and more slender stature separate it from typical specimens of the species. It resembles *Collybia hariolorum* Fr., but differs mainly in its wide lamellae, flexible stipe, and slightly larger spores.

Marasmius rotula Fr. — On dead frondose sticks.

Mycena amabilissima (Pk.) Sacc. — Aside from the slightly smaller spores our plants agree well with the description as given by Beardslee and Coker (1).

Mycena ammoniaca Fr. — Scattered on the fallen leaves of frondose trees.

Mycena cinerella var. **viscida** Kauffman & Smith, var. nov. — Inodora; pileus 5–10 mm. latus, membranaceus, conico-campanulatus, obtusus, brunneo-cinereus, subviscidus, glaber, substriatus; lamellae latae, albido-cinereae, arcuatae, bre-

vissime angulatum decurrentes; stipes 3–4 cm. longus, filiformis, cinereus, apice albido-pulverulentus, subviscidus; sporae ellipsoideae, 7–8 × 4 4.5 μ; cellulae aciei lamellarum clavatae vel apice globosae, leves, 28 × 15 μ. — Specimen typicum in Herb. Mich. conservatum, Kauffman & Smith n. 43, prope Rock River, Michigan, September 10, 1929.

Pileus 5–10 mm. broad and high, membranous, conico-campanulate, obtuse, brownish cinereous, subviscid, glabrous, substriate; lamellae whitish, tinged ashy, ascending arcuate with a decurrent tooth, medium broad, ventricose, edge entire and concolor; stipe filiform, grayish or brownish gray, white pulverulent at apex, subviscid, 3–4 cm. long, 1 mm. thick; spores 7–8 × 4–4.5 μ, elliptical to oblong, smooth; sterile cells globose above, smooth, 15 μ in diameter, 28 μ long with pedicel; basidia 2- and 4-spored. Type collected on sphagnum September 10, 1929, Kauffman and Smith, No. 43. Our plants differed from *M. cinerella* Karst. *sensu* Lange in the gray or brownish gray cap, which is substriate when dry, the lack of odor, non-roughened sterile cells, and subviscid stipe and pileus. It is close to *M. paludicola*, but the spores are smaller, and the stipe is not pure white.

Mycena clavicularis var. cinerea Pk. — Pileus 5–8 mm. broad, conic or hemispheric-campanulate, often papillate, brownish cinereous with a darker umbo, at length subsulcate and shining, dry, glabrous; flesh membranous and concolor; lamellae very narrowly adnexed or almost free, narrow, subdistant, whitish; stipe filiform, about 0.5–0.75 mm. thick, 7–8 cm. long, whitish cinereous, fragile, subviscid, shining when dry, equal and rooting by a prolonged hairy portion which is attached to leaves; odor none; spores 8 × 5 μ, slightly ovate pointed. This plant is close to some members of the Filipedes, namely, *M. vitilis* Fr. *sensu* Lange and *M. filopes* of some American mycologists, but is distinct by its viscid or subviscid stipe. It seems closest to Peck's variety and should be placed there until more information concerning all these species is available.

Mycena corticaticeps Kauffman & Smith, sp. nov. — Pileus 2 4 mm. latus, membranaceus, campanulatus, subpapillatus, pallide vinaceus demum albidus, striatus, glaber; lamellae adnatae, angustae, subdistantes, albidae, acie concolores; stipes 1–3 cm. longus, filiformis, flaccidus, albidus, glaber, radicatus; sporae latae ellipsoideae vel subglobosae, 9–11 × 7–9 μ; cystidia aciculata, ventricosa 45–75 μ. — Specimen typicum in Herb. Mich. conservatum, Kauffman & Smith n. 196, prope Rock River, Michigan, September 20, 1929.

Pileus 2–3 (4) mm. broad, campanulate, subpapillate, faintly vinaceous to dirty pallid, even or translucent striate, glabrous; pileus-trama of three types of tissue, first a layer of very slender horizontal hyaline hyphae, second a layer of coarse brown-walled interwoven cells, and lastly a region of ascending hyaline, more slender hyphae arising from the gill-trama; lamellae adnate, very narrow, subdistant, white; stipe about 2 cm. long, flaccid and filiform, hyaline, white, glabrous, and naked at magnifications of about one hundred and fifty, equal, terete, rooting in the bark of a rotten log by white hairs; spores 9–11 × 7–9 μ, subglobose to very broadly elliptical, hyaline, smooth; sterile cells on the edge 35–45 × 6–11 μ, awl-shaped to ventricose below, hyaline or with tint of lavender; cystidia scattered, 75–80 μ long, otherwise like the sterile cells. This species is distinguished from other small members of the group by its lanceolate awl-shaped cystidia. Type collected on the bark of a rotting hardwood log, September 20, 1929, Kauffman and Smith, No. 196.

Mycena dissiliens Fr. — On a coniferous log. This is a form with rather obtuse pilei, which seems to lack cystidia entirely A large number of collections of the typical specimens have been seen by the authors, and they were all characterized by rather conical pilei and large fusoid-ventricose cystidia. Another collection on frondose wood has since been made in the vicinity of Ann Arbor, which also lacked the typical cystidia, but which otherwise resembles typical specimens rather closely. More data are needed to settle the proper position of the forms listed above.

Mycena epipterygia Fr. — Two collections of this variable plant were made, descriptions of which follow: Pileus 5–10 mm. high and wide, conic-campanulate, obtuse, faintly striate at first, more distinctly so in age, "olive lake," with a paler whitish or yellowish margin or "Naples yellow," at first losing more of the olive and appearing pale yellow when expanded, becoming almost convex, with a thin viscid tough pellicle; lamellae adnate, scarcely toothed, narrow, equal but narrowing in front, moderately subdistant, whitish, edge concolor; stipe 7–9 cm. × 1 mm. or less thick, rooting, or scarcely rooting on bark fragments, pale yellowish to citrine yellow, pellicle viscid; odor slightly spicy or aromatic; spores 11–13 (14) × 6–7 μ, pyriform-ovate, to subellipsoid, hyaline, smooth, basidia bispored, 32 × 7 μ. The second collection had spores 9–11 × 6.5–7.5 μ, short-elliptic to subglobose; basidia 2-spored, sterile cells smooth-capitate; colors and shape as in the first collection; odor weakly fetid; on hemlock logs.

Mycena epipterygia var. B Kauff. — On an old hemlock log.

Mycena filopes Bull. — On débris in frondose woods.

Mycena graveolens Kauffman & Smith, sp. nov. — Aetate marcescens valde odorata, odore iodoformi similis; gregaria; pileus 5–10 mm. latus et altus, conico-campanulatus, fusco-cinereus, membranaceus; lamellae angustae, adnatae, albido-cinereae, confertae; stipes 5–10 cm. longus, 1–1.5 mm. crassus, avellaneus, glaber, flaccide cartilagineus; sporae angusto-ellipsoideae, leves, 8–10 (11) × 4.5–5 (6) μ; cellulae aciei lamellarum subglobosae, asperae; basidia 25 × 5–6 μ, bispora. — Specimen typicum in Herb. Mich. conservatum, Kauffman & Smith n. 173, prope Rock River, Michigan, September 18, 1929.

Pileus 5–10 mm. high and wide, conico-campanulate, sometimes persistently conic-cuculate, "light drab," "tilleul buff," or with a fuscous umbo, fading to a pale drab-gray or "vinaceous-fawn," but umbo persistently darker, often papillate; flesh membranous; lamellae ascending, narrow, linear, slightly

narrowed behind and adnate, no tooth, whitish with a gray tint, close and distinct; stipe 5–10 cm. long, 1–1.5 mm. thick, avellaneous to olive-brown, glabrous, tough, equal, cartilaginous, becoming flaccid, attached to mosses, etc., "ecru-drab" upward, "cinnamon-drab" below, apex white; spores 8–10 × 4.5–5 (6) μ, narrowly elliptical and drawn to a point, smooth; sterile cells enlarged, subglobose on a short narrow pedicel, 18–20 × 13–15 μ, the upper surface is covered by rodlike projections 4–5 μ long; no cystidia; basidia 25 × 5–6 μ, bispored; odor strongly of iodoform after gathering, scarcely present before. Type collected by Kauffman and Smith, No. 173, September 18, 1929, near Rock River, Michigan. This species differs from *M. vitilis* and *M. filopes* in the strong odor which develops after collecting, and also in stature, which, however, is quite variable.

Mycena haematopoda Fr. — Cespitose to gregarious on débris and moss. The spores measured 10–12 × 5–6 μ; the sterile cells, 45–55 × 8–15 μ.

Mycena inclinata Fr. — On frondose logs.

Mycena leajana Berk. — Cespitose on beech logs.

Mycena megaspora Kauffman, sp. nov. — Gregaria, terrestris; pileus 1–4 cm. latus, expansus, umbonatus, fuscus vel fuligineus, demum pallide avellaneus, glaber, lubricus, striatus, cartilagineus; lamellae fuligineae, demum albidae, adnatae vel sinuatae, angustae, ventricosae, subdistantes, confertae; stipes 5–12 cm. longus, 1–3 mm. crassus, cartilagineus, glaber, radicatus; sporae ovato-ellipsoideae 10–12 (15) × 7–8 (9) μ; basidia clavata, bispora; cellulae aciei lamellarum capitatae, asperae. — Specimen typicum in Herb. Mich. conservatum, Kauffman & Smith n. 31, prope Rock River, Michigan, September 9, 1929.

Pileus 1–4 cm. broad, subhemispherical when unexpanded, becoming partly expanded, with a broad, flat, or convex prominent umbo, dark umber to almost black at first, fading through brown in age and finally becoming drab or avellaneous, finely wrinkled-striate, glabrous, lubricous to slightly viscid when fresh; flesh white, 1–1.5 mm. thick, equal nearly

to the edge; lamellae whitish to smoky gray at maturity, very dark when young, adnate or sinuate-uncinate, of narrow to medium width or ventricose and quite broad, subdistant to close, trama parallel, subhymenium distinct; stipe 5–12 cm. × 1–3 mm., with a long rootlike process 5 cm. or more long, brownish or blackish, fistulose, glabrous, even, lubricous, cartilaginous and tough, taste mild or subastringent; odor none; spores 10–12 (15) × 7–8 (9) μ, elliptical, sterile cells 38–40 × 14–22 μ, rough from minute warts; basidia bispored, 52–54 × 7–8 μ; cystidia none. Type collected by Kauffman and Smith near Rock River, Michigan, No. 31. Found growing gregariously on the black muck of swamps, sometimes on sphagnum.

Mycena olivaceo-marginata (Massee) Kühner. — Pileus 7–18 mm. broad, conico-campanulate to campanulate subexpanded, "vinaceous-buff" on the margin, "olive-brown" on the center, various shades between, widely sulcate to the obtuse umbo; flesh concolor, thin; lamellae broadly adnate, subdistant to distant, spuriously joined by an adnate "collar," edge pale olivaceous brownish, faintly intervenose; stipe 2–3.5 cm. × 1–2 mm., strict, terete, tough, whitish, glabrous, even, naked at apex, equal, hollow, attached to the bark of a tamarack stump by radiating white strigose hairs; odor none or very faint; taste mild; spores 9–12 (13–14) × 6–7 (7.5) μ, ellipsoid to ovate, hyaline, smooth to very minutely rough-punctate; sterile cells awl-shaped to subfusiform and tapering to a point, 40–55 × 5–6 μ, hyaline, or filled with olivaceous-brown granules, a few with a dull red content; basidia 4-spored, 36–38 × 7–8 μ, with stout sterigmata.

Mycena parabolica Fr. *sensu* Ricken. — Closely gregarious on leaf mold. The specimens in this collection fit Ricken's description well and should be placed here without a doubt. However, since Lange describes the same species as having a different type of cystidium, it is possible that two species are being classified under the one name.

Mycena pelianthina Fr. — Singly on leaf mold in frondose woods.

Mycena pura Fr. — Gregarious on humus and débris in both coniferous and frondose woods.

Mycena rosella Fr. — In large numbers on conifer needles.

Mycena rubromarginata Fr. *sensu* Bresadola. — Singly on coniferous sticks and bark.

Mycena rugosoides Pk. — Since this species is very seldom collected a complete description seems desirable. Pileus 1.5–3.5 cm. broad, obtusely conic or acorn-shaped, becoming campanulate to expanded, finally nearly plane, "light seal brown" to almost black at first, or "snuff brown," even, upon expanding and losing moisture the color fades to "avellaneous" or pale "vinaceous-buff," long-striate by dark lines while losing moisture, finally dry and wrinkled-striatulate, glabrous, umbo obtuse and prominent; flesh concolor, about 1–1.5 mm. thick; lamellae ascending and narrowly adnate, rounded behind, much broader and ventricose toward the front, 4–5 mm. broad, close to subdistant, whitish at first then cinereous, spotted or entirely rufescent in age, edge entire; stipe 5–7 cm. long, 1.5–2 mm. thick at the apex, 3–4 mm. thick at the base, which is densely white villose, glabrous elsewhere, at first pallid with a tinge of "vinaceous-buff," becoming "fuscous," then paler from the base upward in age, hollow, shining when dry, even; odor none; taste slightly subnauseous; cespitose, often coherent below, on rotten hardwood stumps; spores 7–8 (9) × 4.5–5.5 μ, obtuse, smooth; sterile cells bludgeon-shaped, rounded above, short-spiny, 12–15 × 8–10 μ, cystidia none or few, like the sterile cells; basidia 32 × 5–6.5 μ, 4-spored.

Mycena subviscida Kauffman & Smith, sp. nov. — Pileus 1–2 cm. latus, lentus, late campanulatus, striatus, subviscidus, pallido-avellaneus; lamellae adnatae, ventricosae, angustae, confertae, albidae, acie concolores; stipes 2–3 cm. longus, 1–1.5 mm. crassus, subviscidus, pallidus, glaber; sporae 6.5–8 × 5.5 6 (7) μ, late ellipsoideae vel subglobosae, leves; cellulae aciei lamellarum clavatae, apice asperae. — Specimen typicum in Herb. Mich. conservatum, Kauffman & Smith n. 169, prope Rock River, Michigan, September 18, 1929.

Pileus 1 2 cm. broad, flexible, toughish, broadly campanulate to subexpanded, broadly umbonate in age, striate, appearing whitish but actually a "deep olive-buff," paler toward the margin, shining when wet, subviscid from a thin separable pellicle; flesh thin, white; lamellae adnate, ventricose, rather narrow, close to subdistant, intervenose, whitish, at times joined behind by a spurious "collar," edge entire, concolor; stipe 2–3 cm. × 1–1.5 mm., slightly thickened at the white mycelioid base, tough, slightly viscid, whitish or pallid, pale olive-buff, glabrous, even, equal above, terete, hollow; odor none; taste slight, then subnauseous; spores 6.5–8 × 5.5–6 (7) μ, very broadly ellipsoid or subglobose, hyaline, smooth, obtuse at the ends; cystidia none; sterile cells with an ellipsoid or subglobose head covered by slender rodlike hairs 3–4 μ long, abruptly tapering to a slender pedicel, the whole 35 40 μ long, pedicel 3–4 μ thick, head 9–14 μ thick; basidia 2–3–4-spored, 30 × 8 μ. The type was found growing gregariously on an old aspen log, September 18, 1929. Kauffman and Smith, No. 169.

The smaller spores and the lack of any flesh tints in age distinguish this species from *M. sudora.*

Mycena tenacipes Kauffman & Smith, sp. nov. — Caespitosa; pileus 1–5 cm. latus, conico-campanulatus vel expansus, fuscus, demum avellaneus, hygrophanus, striatus, glaber, non viscidus; lamellae subdistantes, fuligineae, demum pallidae, crassae, adnatae, brevissime angulatim decurrentes; stipes 2 7 cm. longus, 1–3 mm. crassus, albido-pulverulentus, demum glaber, fuscus, cartilagineus; sporae 7 9 × 4 5 μ, ellipsoideae, leves; basidia 35–40 × 5–7 μ; cellulae aciei lamellarum clavatae asperae. — Specimen typicum in Herb. Mich. conservatum, Kauffman & Smith n. 41, prope Rock River, Michigan, September 9, 1929.

Pileus 1–5 cm. broad, conic or acorn-shaped at first, then irregularly campanulate or semioval, at length expanded to repand or campanulate-convex "fuscous" to "bister" when young, becoming "wood brown" to "avellaneous," hygrophanous, when fading with fuscous striae which gradually

disappear, or merely finely wrinkled-striate, glabrous, dry but with a pellicle; flesh thin, hardly 1 mm. thick, equal, concolor; lamellae adnate, thick, often with a slight tooth, close at first, subdistant in age, dark at first, becoming whitish in age, 2–4 mm. broad, edge entire, concolor; stipe 2–7 cm. × 1–3 mm., minutely white pulverulent, terete or compressed, fuscous to "storm gray" when young, becoming paler, glabrous and shining above in age, base white strigose, cespitose, subcespitose or gregarious; taste subrancid, odor none; spores 7–9 × 4–5 μ, ellipsoid-oblong, smooth; basidia 35–40 × 5–7 μ, 2- and 4-spored, sterigmata not prominent; cystidia none, sterile cells bludgeon-shaped, with rodlike projections on the upper part, 18 × 6–11 μ. The type was found growing cespitose to gregarious on very decayed wood and buried material, September 9, 1929. Kauffman and Smith, No. 41. The persistently dark colors and smaller spores distinguish this species from *M. parabolica;* the spores, basidia, habit, and stipe separate it from *M. megaspora.*

Mycena vitilis Fr. *sensu* Kauffman. — On débris in frondose woods.

Mycena vulgaris Fr. — Growing in large numbers on conifer needles. No cystidia or sterile cells were present on these plants.

Mycena vulgaris var. **caespitosa** Kauffman & Smith, var. nov. — Caespitosa; cystidia fusoideo-ventricosa; basidia clavata, bispora; sporae ovatae, 6–7 (8) × 3.5–4 μ. — Specimen typicum in Herb. Mich. conservatum, Kauffman & Smith, prope Rock River, Michigan, September 18, 1929.

Pileus 1–2 cm., convex, obtuse, a few subpapillate, rarely subumbilicate, striatulate, glutinous, colors like those on *M. vulgaris;* lamellae broadly adnate-decurrent, rather broad, whitish; stipe at first whitish, 2–3 cm. × 1–2 mm., glutinous, glabrous, even, subrooting, gregarious to subcespitose on rotten logs; odor none; spores 6–7 (8) × 3.5–4 μ, narrowly ovate-pointed at one end, smooth; sterile cells on edge of gills awl-shaped but obtuse at the apex, some thick; fusiform with a cylindric neck, about 40 μ long, 5–7 μ thick, rare on

the gill surface, basidia 22 × 5-6 μ, bispored; gill-trama of large elongated cells; cespitose on decaying wood. The type was collected on an old log, September 18, 1929, by Kauffman and Smith, near Rock River, Michigan. The larger size, cespitose manner of growth, lignicolous habitat, fusoid-ventricose cystidia, and bispored basidia separate this variety from the species.

NAUCORIA BELLULA Pk. — On very decayed wood, probably coniferous.

NAUCORIA LIGNICOLA Pk. — On rotten wood, probably coniferous.

Naucoria lubriciceps Kauffman & Smith, sp. nov. — Pileus 1.5-3.5 cm. latus, campanulato-convexus vel late umbonatus, lubricus, ochraceo-olivaceus demum fuscus, glaber; lamellae adnatae, brevissime angulatim decurrentes, albidae demum obscure fuscae, latae; stipes 5-6 cm. longus, 3–4 mm. crassus, cylindricus, farctus, innate sericeo-fibrillosus, apice glaber; sporae ovato-ellipsoideae, tuberculosae, 5.5-7 × 3–4 μ; cellulae aciei lamellarum subcylindricae, obtusae, 35 × 6–7 μ. — Specimen typicum in Herb. Mich. conservatum, Kauffman & Smith n. 18, prope Rock River, Michigan, September 8, 1929.

Pileus 1.5–3 (3.5) cm. broad, campanulate, thin, convex, subexpanded, obtuse, broadly umbonate, white hoary when young, lubricous, becoming "cinnamon-buff" to "pinkish cinnamon," tawny-olive blotched with "bister" in age, margin even; pileus trama corticated by a thick layer of compact brownish hyphae, the cells of which are 12–20 μ in diameter and subglobose, the layer 85–125 μ thick, elsewhere the tissue of the loose floccose type, the pileus firm but also rather pliant; flesh watery brownish at first, becoming whitish except the spuriously gelatinous thick surface layer; lamellae adnate with a decurrent tooth, whitish at first, then pinkish buff, finally sordid and darker, close, medium broad, edge entire; stipe 5–6 cm. × 3–4 mm., equal, innately silky, white, fuscescent downward, watery within, then whitish, stuffed, apex naked; spores 5.5–7 × 3-4 μ, subovate to ellipsoid, dark, smooth or nearly so; basidia

25 × 5–6 μ, 4-spored; gill-trama parallel; cystidia none; sterile cells subcylindrical, rounded at the apex, hyaline, short and not prominent, about 35 × 6–7 μ. Type collected under cedars on humus and near moss, near Rock River, Michigan, September 8, 1929, Kauffman and Smith, No. 18. This species is characterized by the subgelatinous upper layer of the pileus, crowded lamellae, sterile cells, and the small spores.

Naucoria melinoides Fr. *sensu* Ricken. — Under *Alnus incana*.

Naucoria obtusissima Kauffman, sp. nov. (Pl. XXXII). — Pileus 6–16 mm. latus, convexus, olivaceus demum flavus, glaber vel atomatus, lubricus; lamellae adnatae, latae, confertae, pallido-flavae; stipes rigidus, 5–9 cm. longus, 1–2 mm. crassus, apice sericeo-fibrillosus et pallidus, basi flavus; sporae 8–10 (11) × 5–6 (7) μ, ellipsoideae, leves; cystidia ventricosa, 42–60 × 8–12 μ. — Specimen typicum in Herb. Mich. conservatum, Kauffman, prope Ann Arbor, Michigan, September 29, 1924.

Pileus 6–16 mm. broad, convex to obtuse, not striate when moist, "deep olive-buff" to "honey yellow," "chamois" in wet weather, glabrous, dull, at length atomate; flesh concolor, thin, soft; lamellae adnate-seceding, broad, close to subdistant, lying down, at length "clay color"; stipe slender, strict, 5–9 cm. × 1–2 mm., stuffed-tubular, whitish and silky-cortinate, becoming "honey yellow" downward, white mycelioid at the base, even at length undulate, flexuous, cartilaginous, concolor within; spores 8–10 (11) × 5–6 (7) μ, dark rusty brown, smooth, ellipsoid; sterile cells present, ventricose with a long subaciculate neck, 42–60 × 8–12 μ; cystidia similar, most abundant near the edge of the lamellae; basidia 2- and 4-spored, 25–28 × 6–7 μ. Type collected by C. H. Kauffman on sphagnum and muck in and around the borders of bogs, Ann Arbor, Michigan, September 29, 1924. This species differs from *N. humidicola* Murr. and from *N. scorpioides* Fr. *sensu* Ricken in its smaller spores, and from *N. myosotis* in its dry pileus as well as smaller spores.

Naucoria sideroides Fr. *sensu* Ricken. — Pileus 8–22 mm.

broad, striate to the obtuse umbo, broadly campanulate to expanded-umbonate, viscid and shining when wet, "tawny" or reddish brown, umbo darker and uneven, glabrous, flesh concolor; trama corticated by a layer of globose or pyriform, pedicellate cells, 17 22 μ in width, brownish, a thin pellicle may be present above this; lamellae adnate, rounded behind, medium broad, tawny cinnamon or tawny ochraceous, close, edge delicately white-fimbriate; stipe 3–4 cm. $\times$ 1.5–2.5 mm., abruptly subclavate bulbillose, concolor throughout, hollow, pallid, shining, even, and glabrous or slightly fibrillose; odor none. The microscopic characteristics fit the species well, but the colors instead of being yellowish were very definitely reddish brown. Color variations are almost the rule instead of the exception, so that it seems best to consider our plants as belonging to the species in the sense of Ricken.

Nolanea conica Pk. — On mosses among conifers. Among the typical specimens were some comparatively large ones with pilei 2–3 cm. broad and very obtuse. However, since the surface markings and microscopic characteristics were similar in both, they no doubt belong to this species. This is probably another instance of gigantic forms similar to those reported for *Lactarius uvidus* in this paper and for *Cortinarius vibratilis* in *The Agaricaceae of Michigan.*

Nolanea mammosa Fr. — On sphagnum.

Nolanea proletaria Fr. *sensu* Ricken. — Pileus 2.5–3 cm. broad, umber brown when moist, scarcely striatulate on the margin, glabrous, even, hygrophanous, broadly flattened but often subumbonate; lamellae broadly adnate, broad, the long ones broader than the alternate shorter sets, sooty brown, edge entire, close to subdistant; stipe 5 cm. $\times$ 2.5 mm., equal, strict, hollow, pale fuscous, innately silky-striatulate, cartilaginous, terete, easily splitting when broken, sometimes compressed; odor slight; taste bitterish to subnauseous; spores globose in outline, 8–9 μ, 5–6-sided but the angles not conspicuous; cystidia and sterile cells none; basidia 28 $\times$ 7–8 μ, 4-spored, gill-trama parallel.

Nolanea versatilis Fr. — In these specimens the sterile cells were not present as cystidia. On humus in damp woods.

Omphalia campanella Fr. — Gregarious on a rotten coniferous log. These plants possessed a small bulb at the base of the stipe, so that this characteristic alone is not enough to distinguish between this species and *O. parvibulbosa.*

Omphalia fibula Fr. — Scattered on mosses.

Omphalia gerardiana Pk. — Singly on sphagnum.

Omphalia parvibulbosa Kauffman & Smith, sp. nov. — Gregaria, terrestris; pileus 5–10 mm. latus, membranaceus, papillatus, convexus demum expansus, umbilicatus, margine striatus; lamellae decurrentes, subdistantes, luteae; stipes 6–8 cm. longus, 1–2 mm. crassus, fusco-ferrugineus, fulvo-hirsutus, bulbosus; sporae 5–6 (7) × 3–4 μ, subcylindraceae, cystidia ignota. — Specimen typicum in Herb. Mich. conservatum, Kauffman & Smith, prope Rock River, Michigan, September 16, 1929.

Pileus 5–10 mm. broad, at first hemispherical, with or without a papilla, flattened-campanulate, expanded plane and then umbilicate, disk "russet" to "tawny," fading to "ochraceous-tawny," margin "warm buff," or "buff-yellow," staining subferruginous in age, when very young pileus covered by a whitish fibrillose pruinosity which disappears in age, umbilicus often slightly hoary; margin faintly to sulcate-striate, usually glabrous and slightly lobed, neither viscid nor hygrophanous; lamellae broadly decurrent, narrowed in front, intervenose, "olive-ocher," "cinnamon-buff" or "deep colonial buff," edge entire; stipe 6 8 cm. × 1–2 mm., date-brown but paler above, covered by a short tawny pubescence, rather abruptly enlarged to a distinct small bulb which is enveloped by a tawny fibrillose covering, solid, concolor within; spores 5–6 (7) × 3–4 μ, hyaline, smooth, obtusely elliptical, basidia 22 × 3.5 4 μ, 4-spored; cystidia none; sterile cells indistinct; gregarious among mosses, especially sphagnum. Type collected by Kauffman and Smith near Rock River, Michigan, September 16, 1929. Found growing gregariously on muck and moss in low areas. This plant might

possibly be classed as *O. campanella* var. *papillata* Fr. or var. *terrestris* Quél., but the distinct habitat, the different habit and stature, smaller spores, and possibly the lack of cystidia distinguish it as a species.

Panus stipticus Fr. — Cespitose to gregarious on hardwood.

Panus torulosus Fr. — On logs of beech and birch.

Paxillus lepista Fr. — Pileus 3–7 cm. broad, convex, becoming depressed in age, whitish, tinged alutaceous or cinnamon-buff, pruinose, soft, innately subtomentose, even on the thin margin, which is narrowly involute, then spreading and sterile; flesh medium thick, 5–7 mm. near the stipe, gradually tapering; lamellae short-decurrent, crowded, 4 6 mm. broad behind, narrowed in front, whitish, becoming arid, separable from the cap-trama, few if any forked, edge thin and entire, in age becoming sordid "ivory yellow" or nearly "pale olive-buff"; stipe central or slightly excentric, about 4 cm. long, elastic but firm within, covered by a thin irregular tomentum, whitish, base ending abruptly, odor subacid, taste bitter or otherwise disagreeable; spores 6–7 (8) × 4.5–5 (6) μ, short-ellipsoid, guttulate, surface with a few scattered tubercles, epispore pink under the microscope. Found growing on débris in a mixed forest of hemlock and birch.

Paxillus tricholoma Schw. — Scattered on humus under second-growth hardwoods.

Pholiota adiposa Fr. — On hardwood logs.

Pholiota aggericola Pk. — On débris in hemlock woods. The pileus was very dark and glutinous.

Pholiota caperata Fr. — Scattered on sphagnum.

Pholiota confragosa Fr. — On débris of frondose wood. The pilei of the plants of this collection fall within the size-range (2–6 cm. broad) as given in *The Agaricaceae of Michigan;* Overholts (21) gives the breadth as 1–2.5 cm.

Pholiota discolor Pk. — On a very rotten log in a mixed forest.

Pholiota squarrosoides Pk. — On beech and maple logs. These specimens were typical for the species.

Pholiota subsquarrosa Fr. (Pl. XXXIII). — Pileus 4–7 cm. broad, fleshy, convex, viscid to glutinous when young or

wet, at first "Pinard yellow" to "empire yellow" becoming "sulphin yellow" where bruised, in age becoming ferruginous from the center out, dotted with concentrically arranged "amber brown" scales about 3 mm. in diameter and triangular near the margin or subconic on the center; margin even, inflexed, and connected with a "straw yellow" cortina, soon appendiculate; flesh of the young plants white to flavescent, moderately compact, thick on the disk, abruptly thin near the margin; lamellae adnate to adnate-emarginate with a tooth, 5–7 mm. broad, crowded, pallid white to "olive-buff" at first, then avellaneous to "clay color" or darker in age, edge minutely white floccose; stipe at first whitish within, covered by the dingy yellowish universal veil which breaks up into scales, flesh lutescent to dingy rufescent toward the base, surface becoming "empire yellow," covered up to the evanescent apical cortinate ring with close-set spreading or pointed yellow scales which darken in age, nearly naked above the annulus; spores 6–7 (8) × 3–4 μ, smooth; cystidia on the sides of the lamellae 30–35 (40) × 7–9 μ, with slender pedicels, ventricose upward and sharply ovate-pointed, scattered, projecting 8–12 μ; sterile cells shorter and obtuse at the apex, quite variable in size; gill-trama parallel. Without a doubt this is the plant which McIlvaine has discussed under this name. The color of the young lamellae in our specimens varied from whitish to "olive-buff," but was never truly yellowish. In this respect our plants agree with the description given by McIlvaine, but not with that given by Fries. However, the type of the scales on the pileus and stipe, their change in color, the viscidity of the pileus, its colors, especially in age, and the markings on the stipe agree essentially with those of our plants.

Pleurotus albolanatus Pk. — On hemlock logs.

Pleurotus inversus Kauffman & Smith, sp. nov. — Pileus 2–4 cm. latus, 3–5 cm. altus, marginatus, semi-infundibuliformis, brunneus, gelatinosus, glaber; lamellae decurrentes, tenues, confertae vel subdistantes; stipes glaber, 1–2 cm. longus, 4–9 mm. crassus, eccentricus; sporae oblongae 6–7 × 2.5–3 μ; cystidia

cylindrica, numerosa, 75–100 × 3–4 μ. — Specimen typicum in Herb. Mich. conservatum, Kauffman & Smith n. 254, prope Rock River, Michigan, September 22, 1929.

Pileus 2–4 cm. broad, 3–5 cm. high, marginate behind, at first spoon-shaped, then semi-infundibuliform or open part way on one side, watery brownish, gelatinous-viscid in wet weather, margin rolled back over the lamellae, glabrous, even; flesh concolor, fading to whitish on drying; lamellae unequally decurrent, 4–5 mm. broad, attenuate to a point on the stem, thin, close but spreading, crisped, edge entire, whitish; stipe excentric to almost lateral at first, 1–2 cm. long, 4–9 mm. thick, tapering downward, equal, curved, subcespitose, pallid, solid, concolor within, glabrous and even, terete, not furrowed; spores 6–7 × 2.5–3 μ, oblong, hyaline; cystidia extraordinary by their abundance and shape, cylindrical, hyaline, obtuse, 75–100 × 3–4 μ; basidia 28 × 5–5.5 μ; gill-trama with undulate-interwoven hyphae; pileus trama of a thick surface of gelatinous hyphae, the tissue otherwise homogeneous and floccose. Type collected on a beech log September 22, 1929, Kauffman and Smith, No. 254, near Rock River, Michigan. This plant corresponds to Ricken's conception of *P. petaloides*, but since Fries described his species as not marginate behind, and since a species answering our plant description is rather well known, it seems best to segregate this as a distinct species. If the European plant proves to be the same, as seems likely, the distribution will include Germany on the basis of Ricken's report.

Pleurotus petaloides Fr. — On a rotten hemlock log.

Pleurotus porrigens Fr. — On conifer logs.

Pleurotus sapidus Kalchb. — On maple logs.

Pleurotus serotinus Fr. — On yellow birch and maple.

Pleurotus sulfuroides Pk. — Pileus 8–10 cm. broad, sterile cells long-pedicellate and oval to ellipsoid, gill-trama parallel.

Pluteus caloceps Atk. — Solitary on a birch stick.

Pluteus cervinus Fr. — On logs of yellow birch, very common.

Pluteus fuliginosus Murr. — Scattered on débris in mixed hemlock and birch forest.

Pluteus granularis Pk. — On a maple stump.

Pluteus pellitus Fr. *sensu* Lange. — On hardwood débris.

Psalliota diminutiva Pk. — Scattered to solitary on humus, in mixed conifer and hardwoods.

Psathyra gossypina Fr. *sensu* Ricken. — On sandy soil; the dull red spores are distinctive.

Psilocybe agrariella Atk. — On partly decayed hardwood débris and leaf mold.

Psilocybe atrorufa Fr. — Scattered to gregarious on a bare area and among mosses.

Psilocybe conissans Pk. — Closely gregarious at the base of a hemlock stub in a birch-hemlock area.

Psilocybe squalidella Pk. — Scattered on sphagnum.

Psilocybe obtusissima Kauffman & Smith, sp. nov. — Pileus 1.5–3 cm. latus, convexus, glutinosus, brunneo-olivaceus demum flavus, hygrophanus; lamellae latea, adnatae, confertae, pallide olivaceae vel ochraceae; stipes 7–9 cm. longus, 2–3 mm. crassus, fuscus, pallido-fibrillosus, cellulae aciei lamellarum cylindricae, obtusae, 50–60 × 5–6 μ; sporae ventricoso-ellipsoideae, 14–18 × 7–8 μ. — Specimen typicum in Herb. Mich. conservatum, Kauffman & Smith n. 142, prope Rock River, Michigan, September 19, 1929.

Pileus 1.5–3 cm. broad, hemispherical to flattened but with a decurved margin, glutinous when wet and fresh, even, "ecru-olive" or "olive-ocher," on losing moisture the colors change to "straw yellow" or a paler yellowish, hygrophanous; flesh concolor, fading to whitish, thin throughout; lamellae very broad, 7–9 mm., broadly adnate, slightly rounded behind, close to crowded, at first pale olive-buff, becoming dark-sprinkled by the spores so that the general effect is a dingy "vinaceous-buff," edge white flocculose; stipe long, slender, equal or slightly thickened toward the base, 7–9 cm. × 2–3 mm., cartilaginous, slightly tough, splitting lengthwise in age, fuscous-drab within, stuffed, hollow or solid near the base, covered by abundant dingy whitish fibrils, even, becoming fragile; odor none; taste slight, then subnauseous; spores 14–18 × 7–8 μ, content olivaceous-tinged,

epispore purple-brown and smooth, ventricose ellipsoid; basidia 42 × 9–11 μ, 2- and 4-spored; sterile cells conspicuous, cylindrical, obtuse, 50–55 (60) × 5–6 μ; cystidia none. Type collected on humus, decaying forest leaves, etc., under bushes, and in mixed hemlock and birch woods, September 19, 1929, Kauffman and Smith, No. 142, near Rock River, Michigan. The glutinous surface dries rapidly, and the cap then becomes subviscid with a distinct pellicle. It differs from *P. uda* in the total lack of an umbo, lack of striations, and smaller spores; from *P. ericaea* in the much larger spores and the presence of abundant white fibrils on the stipe. *P. squalidella* var. *macrospora* Pk. does not have a viscid or subviscid cap and the spores are smaller.

Russula albida Pk. — In mixed hemlock and frondose woods.

Russula aurantialutea Kauff. — On humus in hardwoods.

Russula decolorans var. rubriceps Kauff. — Under hemlock.

Russula delica Fr. — Under conifers.

Russula fallax Cke. — On sphagnum.

Russula flava Rom. — Solitary on humus in hemlock and birch forest.

Russula foetens Fr. — Scattered among hardwoods.

Russula fragilis Fr. — Gregarious on sphagnum.

Russula fulvescens Burl. — On the ground in mixed woods and in a coniferous swamp. The plants in these collections possessed a subacrid taste.

Russula lutea f. vitellina Fr. (*sensu* Kauffman *The Agaricaceae of Michigan*).

Russula optera Burl. — Scattered in a hemlock swamp near black muck and on sphagnum. Pileus "Morocco red" on disk, viscid, faintly tuberculate, rigid, dark vinaceous on the margin, fading in age to light grayish vinaceous with darker patches; lamellae pale yellowish to dingy in age; stipe white, 6 cm. × 10–12 mm., subequal, taste mild to slowly and slightly acrid.

Russula pectinata Fr. — In mixed coniferous and frondose woods.

Russula pulverulenta Pk.

Russula subvelutina Pk. — On humus under frondose trees. Pileus vinaceous brown to maroon on the center, paler toward the margin.

Russula xerampelina Fr. — Under hemlock and birch.

Tricholoma arcuatum Fr. (*sensu* Rea, *Brit. Bas.*, p. 240). — On leaf mold in frondose woods. Lamellae in age dark "ochraceous-buff"; pileus and stipe "clay color."

Tricholoma cerinum Fr. — Under hemlock; easily mistaken for a Naucoria, but the spores are hyaline.

Tricholoma equestre Fr. — On grassy soil under conifers.

Tricholoma fumosiluteum Pk. — Scattered in sphagnum, often almost buried. Pileus 4–6 cm. broad, conic-campanulate, entirely glabrous and even, at length subexpanded and obtusely umbonate or bullate, "mustard yellow," when older or moist with a smoky hue; lamellae whitish or "ivory yellow," medium broad, quite close; stipe whitish becoming sordid, very pale yellowish downward, furfuraceous at the apex, glabrous elsewhere, persistently stuffed; spores 5–6 $\times$ 5 μ, hyaline, globose to subglobose, gill-trama parallel; basidia 42 $\times$ 5–6 μ, long and narrow.

Tricholoma grammopodium Fr. — Pileus 6–12 cm. broad, soon expanded and flattened, firm, "tawny-olive" to alutaceous, the slight, broad umbo fuscous, even, glabrous, pellicle separable when fresh; flesh watery brown becoming whitish when dry, soft, margin inflexed and membranous, spreading in age; lamellae adnate with decurrent lines or merely emarginate, crowded, 6–9 mm. broad, "light pinkish cinnamon" to "pinkish cinnamon" at maturity, brown in age, thin, alternate sets progressively shorter, edge entire, concolor; stipe 6–8 cm. or longer, strict, rigid, rather hard, enlarged to oval, bulbose at base, pallid, becoming sordid, innately fibrillose-silky and longitudinally fibrillose-striate, not furrowed, solid to spuriously hollow, concolor within; odor rancid, often nearly lacking; taste disagreeably farinaceous-rancid; spores 7–9 $\times$ 5–6 μ, ellipsoid, obtuse, hyaline, distinctly rough-punctate; cystidia scattered, fusoid, apex crys-

talloid, 50–55 × 9–11 μ, scattered; basidia 33–35 × 7–8 μ, 4-spored. Found on humus among hardwoods.

TRICHOLOMA LASCIVUM Fr. *sensu* Ricken. — Pileus 5–8 (10) cm. broad, rather thin, convex, obtuse or subdepressed, innately silky, dry, becoming widely and obtusely ribbed toward the margin, often with a few concentrically arranged undulations toward the margin, whitish or tinged alutaceous, "ivory yellow" when fresh, becoming subfragile, margin very thin; flesh 2–3 (4) mm. thick, white, rather soft; lamellae adnate, becoming deeply emarginate-uncinate, whitish, crowded, medium broad to broad behind, narrowed toward the front, flesh color, very thin, lying down, edge entire or uneven; stipe 5–8 cm. × 7–12 mm., subequal but incrassate at the appressed cottony base, mycelioid, solid, white, floccose at the apex, silky or glabrous elsewhere, even; odor strong like that of some species of Inocybe; taste bitter to almost burning; spores 5.5–6 × 3 μ, ellipsoid to oblong, obtuse, punctate-rough under high power; gill-trama parallel. On humus among hardwoods.

TRICHOLOMA MELALEUCUM Fr. *sensu* Ricken. — On humus by a hardwood stump.

TRICHOLOMA PANOEOLUM var. CAESPITOSUM Bres. — Gregarious on humus under second-growth maple.

TRICHOLOMA RUTILANS Fr. — Solitary on coniferous wood.

TRICHOLOMA UNIFACTUM Pk. — Pileus 4–8 cm. broad, convex to plane, whitish or white, in wet weather grayish and mottled by rounded watery spots which are also visible in the unsoaked plants but are less conspicuous, rigid, cuticle cartilaginous and separable, glabrous, slippery when wet; lamellae of young plant adnexed, rounded behind, pure white or dingy, 4–6 mm. broad, abruptly broader behind, thin, edge entire; stipe central, 6–13 × 1–3 cm. thick, cuticle thick, extending above the gill attachment, solid to spongy within, sparsely villose-tomentose, pruinose-silky above; spores 3 4.5 (5) μ, globose to subglobose, minutely echinulate when mature; basidia 28–30 × 5–6 μ, 4-spored. A cespitose plant. One collection on a living maple tree and two collections from

logs in the woods were constant in the characteristics as described. The odor was persistently pleasant, taste slowly subnauseous to bitter.

University of Michigan

Supplementary Note

After this article was in page proof there appeared in *North American Flora* (8*a*) a posthumous monograph by Dr. Kauffman covering the genus Cortinarius, in which *C. clandestinus* and *C. montanus* were described as new (see pages 160 and 164). It has, therefore, been necessary to retain the descriptions in this paper.

A. H. S.

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PLATE XXIII

Cortinarius albidoavellaneus Kauffman & Smith, sp. nov. Type collection, Kauffman and Smith, No. 60, Rock River, Michigan. × 1

PLATE XXIV

Cortinarius bulbosus Fr. × 1

PLATE XXV

Cortinarius clandestinus Kauffman, sp. nov. Mt. Hood, Oregon, October 10, 1922 × 1

PLATE XXVI

Cortinarius confusus Kauffman & Smith, sp. nov. Type collection, Kauffman and Smith, No. 10, Rock River, Michigan. × 1

PLATE XXVII

Cortinarius emolitus Fr. *sensu* Ricken. × 1

PLATE XXVIII

Cortinarius montanus Kauffman, sp. nov. Mt. Hood, Oregon, October 3, 1922. × 1

PLATE XXIX

Cortinarius rimosus Pk. × $\frac{2}{3}$

PLATE XXX

Gomphidius superiorensis Kauffman & Smith, sp. nov. Part of type collection, Kauffman and Smith, No. 92, Rock River, Michigan. × 1

PLATE XXXI

Hygrophorus borealis Pk. × 1

PLATE XXXII

Naucoria obtusissima Kauffman, sp. nov. Rock River, Michigan. × 1

PLATE XXXIII

Pholiota subsquarrosa Fr. × 1

BARK THICKNESS OF SOME MICHIGAN TREES *

CARL D. La RUE

IN SPITE of the numerous data which have been assembled concerning the growth of our forest trees, virtually nothing has been recorded about the rate of growth of the bark. Practical considerations have focused attention on the growth of merchantable timber and, aside from the fact that the bark is necessary to the growth of a tree, it has not received much study. The use of the bark of such trees as chestnut, oak, and hemlock has represented merely an exploitation of natural forest growth, and knowledge of comparative rates of bark production has been unessential.

From a scientific point of view the bark has been given short shrift, and the very word has been considered unscientific and inapplicable by the plant anatomist (1). Phloëm, cortex, periderm, etc., have been studied, though insufficiently as yet; but the bark as a whole has remained a neglected part of our commonest trees.

Though mainly in agreement with the anatomist concerning the scientific use of the word "bark," the author feels that it is often not feasible to separate that part of a tree trunk which lies outside the cambium into components which can be treated scientifically. By accident or design we do remove "bark" from trees; we do use "bark" in tanning, and we shall probably need the term for a long time.

An interest in the rate of growth of bark, which had its origin in studies on *Hevea brasiliensis* (3, 4, 5, 6), the Pará rubber tree,

* Papers from the Department of Botany of the University of Michigan No. 380, reporting work done at the Biological Station of the University of Michigan.

in which the growth and regeneration of bark are of primary importance, has remained with the writer, and has been transferred to trees of a different zone. One does not often have an opportunity to secure any considerable number of data on bark thickness, but the felling of a primeval beech-maple-hemlock forest near Pellston, Michigan, in 1928 and 1929 enabled the writer to secure the measurements on *Acer saccharum*, *Fagus grandifolia*, *Tsuga canadensis*, and *Betula lutea* presented in this paper. In 1931 improvement thinnings near the Biological Station of the University of Michigan made possible the studies on *Quercus borealis*, *Acer rubrum*, *Populus grandidentata*, and *Populus tremuloides*.

STUDIES OF SPECIES

Tsuga canadensis

The hemlock trees in the tract were magnificent specimens; most of them were of great age and large size. Gates and Nichols (2) made a study of their ages and diameters and found that they ranged in age from 10 to 400 years and in diameter from 10 to 100 centimeters. More than half of them were over a hundred years old.

Observations on hemlock are of special interest because the bark is employed in tanning, a use to which the bark from the trees in question was put. In some instances the bark was pried from part of the stump, as well as from the trunk after the tree was felled, so that a measurement of bark thickness had to be taken at the highest level of the remaining bark rather than at the top of the stump. Trees from which the bark had been removed down to the root crown are not included in this study.

The stumps varied from 50 cm. to 1 m. in height; and, since measurements of diameter were made on the top of the stump and those of bark thickness at the same level, wherever possible, some variation due to different levels of measurement was introduced. Most of the trees, however, did not taper rapidly, and the error due to this condition is probably not important.

It was not possible to estimate the amount of outer bark which had been lost; in a consideration of the rate of growth this

would have been desirable. But the hemlock does not shed any of its outer bark, and the loss by decay must be very slight in a tissue so full of tannin as this. Hence we may assume that the distance from the cambium to the outer limit of the thickest wedge of bark represents nearly all the growth which has taken place. Evidence from other sources shows the high resistance to decay exhibited by bark of hemlock; and the fact that the hemlock forms bark at a low rate, yet bears the thickest bark of all Michigan trees, proves that it is thick only because so little of it is ever lost.

The data secured from these trees are given in Table I. The greatest thickness of bark, 53 mm., is remarkable in comparison with that of most trees. It is unfortunate that age counts could not be made at the time the other measurements were made. Gates and Nichols present diameter–age figures which show that a tree of the size of this one (100 cm. in diameter), should have an age of more than 300 years. At such a rate of growth the yearly bark increment would be 0.177 mm. Another tree only 79 cm. in diameter might have an age of only 200 years, though it also might be 300 years old. If we take the lower figure, we find a mean annual increment of bark of 0.265 mm. The average diameter for all the trees is 56.13 cm.; from Gates and Nichols' table we find that trees of such a size range in age from 100 to 300 years. If we assume an average age of 200 years, we arrive at 0.125 mm. as a mean annual bark increment. There can hardly be any question of the slow growth of hemlock bark. The use of the results of Gates and Nichols is less questionable than the application of such data would be in general, because a majority of the trees which they measured are represented again in the data in Table I.

The correlation between diameter and bark thickness was computed, not from Table I, but from data on individual trees, by the use of a tabulating and calculating machine, operated by members of the Sorting and Tabulating Station of the University of Michigan. The bark thickness is 4.47 per cent of the diameter.

TABLE I

RELATION BETWEEN DIAMETER AND BARK THICKNESS IN *TSUGA CANADENSIS*

Diameter in cm.	Bark thickness in mm.																									
	5-6	7-8	9-10	11-12	13-14	15-16	17-18	19-20	21-22	23-24	25-26	27-28	29-30	31-32	33-34	35-36	37-38	39-40	41-42	43-44	45-46	47-48	49-50	51-52	53-54	Total
6–10	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1
11–15	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1
16–20	..	..	4	1	2	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	10
21–25	..	1	..	..	1	..	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	4
26–30	..	..	..	1	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2
31–35	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1
36–40	..	1	..	1	..	1	1	2	2	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	10
41–45	..	..	..	..	1	2	2	6	..	2	2	1	..	2	..	..	..	..	..	..	..	..	..	..	..	18
46–50	..	..	..	..	..	2	2	3	3	3	..	2	..	3	1	..	..	..	..	..	..	1	..	..	..	20
51–55	..	..	..	..	1	1	1	4	1	4	1	2	2	2	..	..	2	..	1	..	..	..	..	..	..	22
56–60	..	..	..	..	..	1	2	2	3	3	1	..	3	1	..	..	1	..	..	..	..	..	..	..	..	17
61–65	..	..	..	..	..	..	..	1	3	2	2	1	2	2	..	..	1	..	..	..	..	..	..	..	..	14
66–70	..	..	..	..	..	..	..	1	2	1	1	2	2	1	..	..	1	..	..	..	1	..	..	..	..	12
71–75	..	..	..	..	..	..	..	1	..	1	..	2	..	..	1	..	1	1	1	..	1	..	..	..	..	9
76–80	..	..	..	..	..	..	..	..	1	1	..	..	2	..	2	1	2	1	..	..	..	..	1	..	1	12
81–85	..	..	..	..	..	..	..	..	..	2	..	2	1	..	2	1	..	1	1	..	..	..	..	..	..	10
86–90	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	1
91–95	..	..	..	..	..	..	..	..	..	..	..	2	..	2	..	..	..	..	..	..	..	..	..	..	..	4
96–100	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	1
101–105	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0
106–110	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	1
Total	2	2	4	3	5	11	10	20	15	22	7	14	12	13	7	2	8	4	3	0	2	1	1	0	2	170

Average diameter = 56.13 cm.
Average thickness of bark = 25.12 mm.
Correlation between diameter and bark thickness = + 0.689.

Betula lutea

The trees of *Betula lutea* included in this study were interspersed among the hemlocks considered above. The data were secured in the same way as those for the hemlock, except that none of the bark had been removed and that slight source of error was eliminated. The bark of the yellow birch does not break up into wedges as does that of the hemlock, but cracks into broad thin plates. Some of the first-formed bark, which is silvery yellow-gray, peels off and is lost, but the actual thickness of the part lost cannot be great, though it may not be negligible.

TABLE II

RELATION BETWEEN DIAMETER AND BARK THICKNESS IN *BETULA LUTEA*

Diameter in cm.	Bark thickness in mm.																		
	1–2	3–4	5–6	7–8	9–10	11–12	13–14	15–16	17–18	19–20	21–22	23–24	25–26	27–28	29–30	31–32	33–34	35–36	Total
16–20	1	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2
21–25	..	..	1	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	2
26–30	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0
31–35	..	..	..	3	4	3	..	..	..	..	..	..	..	..	..	..	..	..	10
36–40	..	..	..	4	1	3	..	..	3	..	..	..	..	..	..	..	..	..	11
41–45	..	..	..	..	..	..	2	3	1	..	..	..	..	..	..	..	..	..	6
46–50	..	..	..	..	1	..	1	1	..	1	1	..	..	..	..	..	..	..	5
51–55	..	..	..	..	1	1	1	3	..	1	2	..	..	..	..	..	..	..	9
56–60	..	..	..	..	..	..	..	..	2	..	..	..	..	..	..	..	..	..	2
61–65	..	..	..	..	..	1	..	1	..	..	1	..	..	..	..	..	..	..	3
66–70	..	..	..	..	..	..	..	1	..	..	..	1	..	..	..	..	..	..	2
71–75	..	..	..	..	..	..	..	..	1	1	..	1	..	..	..	..	..	..	3
76–80	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	1
81–85	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0
86–90	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	1
Total	1	0	2	7	8	8	4	9	8	3	4	2	0	0	0	0	0	1	57

Average diameter = 45.72 cm.
Average thickness of bark = 13.83 mm.
Correlation between diameter and bark thickness = + 0.796.

Table II presents the data secured for *Betula lutea*. The trees were nearly as large as the hemlocks, but the bark is a great

deal thinner, being on the average only 3.03 per cent of the diameter. Gates and Nichols did not study this species, and we have no data on the age of the trees in this tract.

The correlations between diameter and bark thickness were calculated from individual tree measurements in the same way as for the hemlock.

TABLE III

RELATION BETWEEN DIAMETER AND BARK THICKNESS IN *ACER SACCHARUM*

Diameter in cm.	Bark thickness in mm.																								
	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	Total
11–15	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
16–20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0
21–25	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
26–30	.	.	.	.	1	.	1	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	4
31–35	.	.	.	1	1	1	4	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	9
36–40	.	.	.	.	4	.	.	3	.	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	10
41–45	.	.	.	.	.	2	.	2	.	1	1	.	.	1	1	.	.	.	.	.	.	.	.	.	8
46–50	.	.	1	1	1	.	.	1	.	1	1	1	.	.	1	.	.	.	.	.	.	.	.	.	8
51–55	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	2
56–60	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	1	.	.	.	.	.	1	4
61–65	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
66–70	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1
71–75	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0
76–80	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0
81–85	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	1
Total	1	0	1	2	7	3	5	8	2	7	4	1	2	2	3	1	0	1	0	0	0	0	0	1	51

Average diameter = 42.87 cm.
Average bark thickness = 13.21 mm.

Acer saccharum

The trees of *Acer saccharum* were growing among the hemlocks and yellow birches in the Pellston tract. Measurements were made in the same way as for the preceding species. Data for bark thickness and diameter are given in Table III.

In Acer there is little tendency for the outer bark to flake off,

but on very old trees the amount of weathering may be significant, though it proceeds very slowly, so far as one may judge from superficial observation.

The bark of the sugar maple is of almost the same thickness relative to the diameter as that of the yellow birch, being 3.08 per cent of the diameter. In trees of the average size shown in Table III, 42.87 cm., Gates and Nichols (2) record a range of age from 50 to 250 years, with the greatest number of this size-class in the 151 200 year-age class. If we assume an average age of 150 years, the mean annual bark increment would be 0.088 mm. The tree with the thickest bark (28 mm.) is 56 cm. in diameter. According to data from Gates and Nichols' tables, it might be as young as 100 years or as old as 300 years. If we assume the more youthful figure for it, the mean yearly increase in bark thickness would be 0.28 mm.

The coefficient of correlation between bark thickness and diameter was not calculated because of the small number of variates, but Table III indicates a fairly high correlation, though probably it would not be so high as that of hemlock, or of yellow birch, unless the addition of other variates changed the pattern considerably.

Fagus grandifolia

For a beech-maple-hemlock forest the beech component of the Pellston area was decidedly small. At the time the measurements were made it was not realized that data had been secured on so few trees of this species; otherwise, a larger number would have been sought out.

The bark of the beech is interesting because it does not contain cork (1) and, partly as a consequence of this, is thinner than that of any other local tree of a similar size. The outer bark does not scale, and weathering affects it very little. An evidence of this is the existence of leaf scars on trunks a century old. Hence, thin as it is, the bark on an old tree represents very nearly all that has ever been formed.

Measurements were made as in the other species, but probably with greater accuracy because of the smoothness of the surface

of the bark. The data are given in Table IV. Age counts were not made on these trees, and therefore we have no basis for estimation of the growth rate of the bark. The bark thickness is

TABLE IV

Relation between Diameter and Bark Thickness in *Fagus grandifolia*

Diameter in cm.	Bark thickness in mm.																		Total
	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	
15–16	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1
17–18	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1
19–20	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0
21–22	..	1	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	2
23–24	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0
25–26	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0
27–28	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0
29–30	..	..	1	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	2
31–32	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1
33–34	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0
35–36	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0
37–38	..	..	..	..	..	1	..	1	1	..	..	..	..	..	..	..	..	..	3
39–40	..	..	..	..	..	..	..	..	..	..	1	..	1	..	..	..	..	..	2
41–42	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0
43–44	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	1
45–46	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0
47–48	..	..	..	..	1	..	..	..	..	..	..	..	1	..	..	..	..	..	2
49–50	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0
51–52	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	1	2
Total	2	1	1	1	1	4	0	1	1	0	1	0	2	0	1	0	0	1	17

Average diameter = 35.38 cm.
Average bark thickness = 8.59 mm.

only 2.42 per cent of the diameter, the lowest percentage shown by any species considered in this work.

Populus grandidentata

Populus grandidentata and the three following species were studied in an oak-maple-aspen wood, consisting mostly of second-

ary growth, near the Biological Station. The trees examined were felled in improvement thinnings, and usually were cut very near the ground. The lowest measurements and the age counts were made at approximately the lowest points on the trunks above the swellings of the root crowns. In these four species the bark showed little fissuring, and where fissures had formed, the bark measurements were made from the cambium to the outer surfaces of the flat plates between the fissures. In this way measurements were secured which are probably more accurate than those made on rough, old bark can be. It is desirable that they should be accurate, since the values are relatively small. Diameter measurements were made with calipers, and were taken through the greatest diameter of the trunk whenever any noticeable variation in the width of the trunk appeared.

Table V contains the data on diameter and bark thickness secured for *Populus grandidentata.* The trees concerned were relatively young, although much older trees, which have grown to greater size and have produced much thicker bark, are fairly common in the species. It is felt, however, that the data are more significant than those from the older trees would be, because the trees concerned are more representative of the species as it occurs in the forest than are the rarer, old ones. Trees of this species are short-lived, and usually die before they have reached an age beyond that of the oldest ones included in this study.

The correlation between diameter and bark thickness is much lower than that in the hemlock or the yellow birch. The bark appears thin, but is not thin relatively to the diameter, since it is 5.81 per cent of that figure. In Table VI the relation between age and diameter is given for *Populus grandidentata;* in Table VII, that between age and bark thickness. From the latter table it appears that growth rate of the bark is considerably higher than that estimated for hemlock or for sugar maple. The most rapid growth rate for a single tree of *Populus grandidentata* was 0.60 mm. yearly. In these cases we have, not estimates, but calculated values. Tables VI and VII show that there is little correlation between age and either diameter or bark thickness. One might expect that conditions which suppressed one of these

TABLE V

RELATION BETWEEN DIAMETER AND BARK THICKNESS IN *POPULUS GRANDIDENTATA*

Diameter in cm.	Bark thickness in mm.											
	2	3	4	5	6	7	8	9	10	11	12	Total
3	1	..	..	..	..	..	..	..	..	..	..	**1**
4	..	1	..	..	..	..	..	..	..	..	..	**1**
5	..	..	1	..	..	..	..	..	..	..	..	**1**
6	..	1	1	1	1	3	..	..	..	..	..	7
7	..	..	..	..	1	2	1	..	..	..	..	4
8	..	1	..	1	..	..	..	..	..	..	..	2
9	..	1	1	..	4	..	1	..	..	..	..	7
10	..	..	..	2	1	..	..	..	..	..	..	3
11	..	..	..	1	2	4	3	..	..	..	..	10
12	..	..	..	2	1	4	3	2	..	..	..	12
13	..	..	..	1	1	..	1	3	..	..	..	6
14	..	..	..	..	1	1	2	3	..	..	..	7
15	..	..	..	..	..	4	..	1	..	..	..	5
16	..	..	..	1	1	1	..	..	..	..	1	4
17	..	..	..	..	..	..	..	..	1	..	1	2
18	..	..	..	..	..	..	..	1	..	..	..	1
19	..	..	..	1	..	..	..	..	..	..	..	1
20	..	..	..	..	..	..	2	..	..	..	..	2
21	..	..	..	..	..	..	..	..	..	..	..	0
22	..	..	..	..	..	..	..	..	..	1	..	1
Total	1	4	3	10	13	19	13	10	1	1	2	77

Average diameter = 11.82 cm.
Average thickness of bark = 6.87 mm.
Correlation between diameter and bark thickness = + 0.499.

TABLE VI

RELATION BETWEEN AGE AND DIAMETER IN *POPULUS GRANDIDENTATA*

Age in years	Diameter in cm.																				Total
	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	
13	..	..	..	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2
14	1	..	1	..	..	..	..	..	2	1	1	..	..	1	..	..	..	..	..	..	..	7
15	..	..	..	..	1	2	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	4
16	..	..	..	..	..	..	..	..	..	3	..	1	2	1	..	..	..	..	..	..	..	7
17	..	..	..	..	1	..	..	1	1	..	3	..	..	2	..	..	..	..	..	..	..	8
18	..	..	..	..	1	..	..	..	..	3	2	1	1	1	..	..	..	..	..	..	..	9
19	..	..	..	..	1	1	..	1	..	2	1	1	1	..	..	..	..	..	..	..	..	8
20	..	..	..	..	1	1	..	1	1	..	2	1	..	..	..	1	1	..	2	..	1	12
21	..	..	..	1	..	..	..	..	..	2	1	1	..	..	..	..	..	..	..	..	..	5
22	..	..	..	..	..	..	1	1	..	..	1	..	..	..	1	..	..	..	..	..	..	4
23	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1
24	..	..	..	..	..	..	1	..	..	..	..	..	1	..	..	..	..	..	..	..	..	2
25	..	..	..	..	..	..	1	..	..	..	..	..	1	..	..	..	..	..	..	..	..	2
26	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0
27	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0
28	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0
29	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0
30	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	1
31	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	1
32	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	1
33	..	..	..	..	..	..	..	..	..	1	..	..	..	..	1	..	..	..	..	..	..	2
Total	1	0	1	2	7	4	3	6	5	12	11	5	7	5	2	1	1	0	2	0	1	76

Average age = 19.19 years.

TABLE VII

RELATION BETWEEN AGE AND BARK THICKNESS IN *POPULUS GRANDIDENTATA*

Age in years	Bark thickness in mm.																					
	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	Total
13	..	..	..	..	1	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	2
14	1	..	1	..	..	1	..	..	1	2	1	..	..	..	..	..	..	..	..	..	..	7
15	..	..	..	1	..	..	..	..	1	..	..	1	..	1	..	..	..	..	..	..	..	4
16	..	..	..	..	..	..	..	..	1	..	3	..	2	..	1	..	..	..	..	..	..	7
17	..	..	..	1	..	..	..	..	1	1	2	1	..	1	..	1	..	..	..	..	..	8
18	..	..	..	..	..	..	..	..	..	1	2	2	1	1	1	1	..	..	..	..	..	9
19	..	..	..	..	..	1	..	..	..	1	..	..	2	3	..	1	..	..	..	..	..	8
20	..	..	..	..	..	..	1	1	1	..	1	2	2	..	1	1	..	..	1	..	1	12
21	..	..	..	..	..	..	..	..	1	..	1	..	1	1	1	..	..	..	..	..	..	5
22	..	..	..	..	..	..	1	..	1	..	..	..	..	..	1	..	..	..	..	..	..	3
23	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1
24	..	..	..	1	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	2
25	..	..	1	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	2
26	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0
27	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0
28	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0
29	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0
30	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	1
31	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1
32	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	1
33	..	..	..	..	..	..	..	1	..	..	..	1	..	..	..	..	..	..	..	..	..	2
Total	1	0	2	3	1	3	3	3	7	6	11	8	8	7	5	5	0	0	1	0	1	75

Average age = 19.19 years.
Average bark thickness = 6.93 mm.
Average annual bark increment = 0.36 mm.

would have a similar effect on the other; but it is surprising, in view of these two tables, that correlation between diameter and bark thickness should be so low. The coefficient of correlation was calculated from data for individual trees, and in the same way as that for the hemlock, so that it is unlikely that any mistake has been made.

Quercus borealis

The data from the few trees of *Quercus borealis* which were available for study are given in Tables VIII and IX. It appears from these tables that there is a lack of correlation between age and diameter and between age and bark thickness, as in the preceding species. The bark thickness represents 5.49 per cent of the diameter, nearly as great a value as that for *Populus grandidentata*, but the rate of bark growth is much lower than for that species. The greatest rate of bark increase for a single tree is 0.45 mm. per year.

Populus tremuloides

Measurements made on a few trees of the quaking aspen are shown in Table XI. The yearly bark increment is very small, only 0.17 mm., and the most rapid bark growth for a single tree is only 0.31, also a low value. The percentage of bark to diameter averages 6.1, the highest for any species included here, although one single small tree has a bark thickness which is 11.1 per cent of its diameter.

Acer rubrum

Table XII gives the data secured for *Acer rubrum*. The bark is very thin, but all the trees measured were small, and the percentage of bark to diameter is not so low as in some other species, being 4.0. The greatest percentage of bark for an individual tree is 5.5. The yearly bark increment is very low, 0.11 mm., and the tree with most rapid bark growth shows an annual increment of only 0.19 mm.

BARK THICKNESSES AT DIFFERENT HEIGHTS ON THE TRUNK

The rate at which bark thickness decreases from the root crown upward could be a matter of economic interest only in such

TABLE VIII

Relation between Age and Diameter in *Quercus borealis*

Age in years	Diameter in cm.																							Total
	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	
21–22							1																	1
23–24	1																							1
25–26	1	1																						2
27–28																								0
29–30																								0
31–32											1													1
33–34									1						1				1					3
35–36													2											2
37–38																								0
39–40																							1	1
41–42										1							2							3
43–44																								0
45–46									1															1
47–48																								0
49–50																								0
51–52															1									1
53–54																	1		1					2
Total	2	1	0	0	0	0	1	0	2	1	1	0	2	0	2	0	3	0	2	0	0	0	1	18

Average age = 37.1 years.
Average diameter = 17.3 cm.

TABLE IX

RELATION BETWEEN AGE AND BARK THICKNESS IN *QUERCUS BOREALIS*

Age in years	Bark thickness in mm.																					Total
	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	
21–22			1																				1
23–24	1																						1
25–26			1		1																		2
27–28																							0
29–30																							0
31–32			1																				1
33–34								2								1							3
35–36				2																			2
37–38																							0
39–40																	1						1
41–42						1		1					1										3
43–44																							0
45–46					1																		1
47–48																							0
49–50																							0
51–52										1													1
53–54																	1					1	2
Total	1	0	3	2	2	1	0	3	0	1	0	0	1	0	0	1	2	0	0	0	0	1	18

Average age = 37.1 years.
Average bark thickness = 9.5 mm.
Average annual bark increment = 0.256 mm.

plants as hemlock, cinnamon, cinchona, and the Pará rubber tree. Thus far it has been investigated only in the last of these, in which it has some bearing on the height to which trees may be tapped advantageously. In our native trees it may be considered only a matter of scientific curiosity to wish to know whether the relation of bark to trunk diameter is the same in the upper parts of the tree as it is in the lower trunk.

A study of this relation was made in *Populus grandidentata*, *P. tremuloides*, *Acer rubrum*, and *Quercus borealis*. The results are presented in Tables X–XIII. Measurements of diameter were taken with tree calipers, and bark measurements were made on small pieces of bark which had been chopped out at appropriate levels. Counts of annual rings were made at the bases of the trees very near the ground level.

In all four species the bark thickness decreases rapidly from the ground level to a height of one meter, and at a lesser and declining rate above one meter. The diameters of the trees decrease at a rather uniform rate, though the rate differs with the various species. *Quercus borealis* shows a more rapid taper of the bole than do the other three types.

The percentage relation of bark to diameter reveals a rapid decrease from the ground level to a height of one meter, except in *Acer rubrum*, which has the lowest percentage at a height of four meters. All species increase in this percentage at higher levels, and in *Populus grandidentata* and *Acer rubrum* the percentage becomes greater at the upper levels than it was at the ground. In all the species there are individual trees with a greater percentage of bark at the upper end of the trunk than at the lower. Trees of which the boles taper slowly and uniformly have less variation in percentage of bark to trunk than those with a more rapid decrease in diameter.

DISCUSSION

It is unfortunate for such a study as this that stands of trees of even age are not ordinarily available. Bark thickness cannot be determined without some damage to the trees, though the damage need be no greater than that caused by increment borings.

In *Hevea brasiliensis*, the only species in which bark growth has been studied to any extent, the bark is relatively soft and permits the use of measuring instruments, developed by the writer and others, which probe through the bark and determine its thickness. On hard-barked trees, however, such devices are of no use, and substitutes for them have not been developed.

The lack of economic value of the bark of most local species has led to a dearth of interest in the study of bark growth, and many opportunities for such study have been neglected. It is to be hoped that, in the future, measurements of the bark will be made when uniform stands of trees are felled.

The hemlock tree produces the most valuable bark of all Michigan trees, though the amount of such bark available in the state is probably small at the present time, and there seems no likelihood that it will ever become desirable to cultivate the tree for this product. Its bark is thicker than that of any other local tree, but it grows very slowly and becomes thick only because of its resistance to decay and because it does not flake off to any considerable extent. The only comparison that can be made with the bark of the old hemlock trees is that of the oldest trees of *Hevea brasiliensis* in the Amazon Valley (6), some of which are older than any of the hemlocks which grew on the Pellston tract. In old age the Hevea tree sometimes has a thick bark as compared with that of most tropical trees, but the thickest bark found there is much thinner than that of the oldest hemlock trees.

In the range of bark thickness the beech stands at the opposite end from the hemlock. It is of interest to note how very little bark is needed for the successful growth of a large tree. However, the average thickness of bark on 174 untapped trees of *Hevea brasiliensis* measured in Matto Grosso, Brazil (6), was only 7.0 mm. In Sumatra (3) 1,063 ten-year-old trees had a mean bark thickness of 7.5 mm., and another plot of 1,004 trees of the same age (5) showed a mean bark thickness of 9.05 mm. Comparatively, then, the bark of the beech is not remarkably thin. Of our native trees the beech is most like the majority of tropical trees in the absence of cork formation; and it is the cork which gives most of the thickness to the bark of trees of the temperate zone.

TABLE X

DATA ON *POPULUS GRANDIDENTATA*

Diameters are given in cm.; bark thicknesses in mm.

Tree no.	Age	Height of Measurement														
		Ground			1 meter			2 meters			3 meters			4 meters		
		Diam.	Bark	Per cent Bark	Diam.	Bark	Per cent Bark	Diam.	Bark	Per cent Bark	Diam.	Bark	Per cent Bark	Diam.	Bark	Per cent Bark
1	14	4.2	3.0	7.1	3.2	1.5	4.7	2.4	1.3	5.3	....	...	...	....	...	...
2	14	2.5	2.0	8.0	1.7	1.0	5.9	0.8	0.5	6.3	....	...	...	....	...	...
3	33	11.5	5.3	4.6	10.5	4.5	4.3	8.8	4.5	5.0	7.0	4.3	6.1	5.8	3.8	6.8
4	38	17.5	10.0	5.7	14.5	7.0	4.8	13.0	7.0	5.4	11.5	7.0	6.1	10.0	4.5	4.5
5	33	16.0	7.5	4.7	15.0	6.5	4.3	14.5	7.0	4.8	11.0	6.0	5.4	8.0	5.0	6.3
6	23	6.3	5.0	7.9	6.0	2.5	4.1	5.3	2.0	3.8	4.5	2.0	4.4	....	...	...
7	13	5.5	4.0	7.3	4.3	2.5	5.9	3.3	1.1	5.3	....	...	...	....	...	...
8	15	6.0	3.8	6.3	4.5	2.3	5.0	4.0	2.0	5.0	....	...	...	....	...	...
9	31	9.3	4.5	4.8	7.0	3.5	5.0	5.5	3.5	6.4	4.3	2.5	5.8	....	...	...
10	17	6.5	3.5	5.4	5.5	3.0	5.5	4.5	2.5	5.5	3.5	2.0	5.7	....	...	...
11	32	10.5	5.5	5.2	9.3	3.8	3.0	8.0	3.5	4.4	6.5	3.0	4.6	5.5	2.5	4.5
12	24	8.0	3.5	4.4	6.5	2.5	3.8	6.0	2.0	3.3	5.0	1.8	3.6	4.3	1.5	3.5
13	30	14.0	9.5	6.8	12.0	4.5	3.8	11.0	4.3	3.9	9.5	4.0	4.2	8.3	3.5	4.1
14	40	19.5	20.0	10.2	16.5	12.5	7.5	15.0	6.0	4.0	13.5	6.0	4.4	13.5	5.5	4.1
15	25	8.8	3.0	3.4	7.0	2.5	3.6	6.5	2.0	3.1	6.0	2.0	3.3	5.0	1.8	3.6
16	54	14.5	9.5	6.6	14.0	7.5	5.4	13.3	7.5	5.6	13.0	6.5	5.0	11.5	6.5	5.7
17	54	13.5	5.5	4.1	13.0	4.8	3.5	11.5	4.5	3.9	11.0	4.0	3.9	9.5	4.3	4.5
18	52	21.0	10.5	5.0	19.0	5.5	2.9	18.0	6.0	3.3	16.0	5.0	3.1	14.0	5.0	3.6
19	49	18.5	12.0	6.8	16.0	5.5	3.4	15.0	5.0	3.3	14.0	4.5	3.2	12.5	4.0	3.2
Averages	31.1	11.2	6.7	6.0	9.8	4.4	4.5	8.8	3.8	4.1	9.1	4.0	4.4	9.0	3.9	4.3

Average growth in diameter per year = 0.360 cm.
Average annual bark increment = 0.215 mm.

DATA ON *POPULUS GRANDIDENTATA*

Diameters are given in cm.; bark thicknesses in mm.

Tree no.	Age	Height of Measurement														
		5 meters			6 meters			7 meters			8 meters			9 meters		
		Diam.	Bark	Per cent Bark	Diam.	Bark	Per cent Bark	Diam.	Bark	Per cent Bark	Diam.	Bark	Per cent Bark	Diam.	Bark	Per cent Bark
1	14	....	...	...	...	...	...	...	...	...	...	...	...	...	...	...
2	14	....	...	...	...	...	...	...	...	...	...	...	...	...	...	...
3	33	....	...	...	...	...	...	...	...	...	...	...	...	...	...	...
4	38	8.5	4.0	4.7	7.0	3.5	5.0	6.0	2.5	4.2	4.0	2.5	6.3	2.5	2.0	8.0
5	33	4.0	2.0	5.0	2.0	1.5	7.5	1.0	0.8	7.5	...	...	...	...	...	...
6	23	....	...	...	...	...	...	...	...	...	...	...	...	...	...	...
7	13	....	...	...	...	...	...	...	...	...	...	...	...	...	...	...
8	15	....	...	...	...	...	...	...	...	...	...	...	...	...	...	...
9	31	....	...	...	...	...	...	...	...	...	...	...	...	...	...	...
10	17	....	...	...	...	...	...	...	...	...	...	...	...	...	...	...
11	32	4.5	2.0	4.4	3.5	1.8	5.0	...	...	...	...	...	...	...	...	...
12	24	2.5	1.0	4.0	...	...	...	...	...	...	...	...	...	...	...	...
13	30	7.0	3.0	4.3	5.0	2.5	5.0	3.8	2.0	5.8	...	...	...	...	...	...
14	40	9.3	4.8	5.2	7.5	3.5	4.7	6.5	3.0	4.6	5.0	2.8	5.6	...	...	...
15	25	4.5	1.8	4.0	3.5	1.5	4.3	2.5	1.0	4.0	...	...	...	...	...	...
16	54	9.5	4.5	4.7	7.5	3.3	4.4	6.5	3.0	4.6	5.5	2.5	4.5	4.0	2.3	5.8
17	54	9.0	3.8	4.2	7.5	3.5	4.7	6.5	3.0	4.6	5.0	2.5	5.0	4.0	2.5	6.3
18	52	12.0	4.5	3.8	8.5	3.3	3.9	6.0	2.8	4.7	4.5	2.0	4.4	...	...	...
19	49	9.0	3.5	3.9	7.5	2.5	3.3	6.0	2.5	4.2	4.3	1.5	3.7	...	...	...
Averages	31.1	7.3	3.2	4.4	5.9	2.7	4.6	5.0	2.3	4.6	4.7	2.3	4.9	3.5	2.3	6.6

Average growth in diameter per year = 0.360 cm.
Average annual bark increment = 0.215 mm.

TABLE XI

DATA ON *POPULUS TREMULOIDES*

Diameters are given in cm.; bark thicknesses in mm.

Tree no.	Age	Height of Measurement																							
		Ground			1 meter			2 meters			3 meters			4 meters			5 meters			6 meters			7 meters		
		Diam.	Bark	Percent Bark	Diam.	Bark	Percent Bark	Diam.	Bark	Percent Bark	Diam.	Bark	Percent Bark	Diam.	Bark	Percent Bark	Diam.	Bark	Percent Bark	Diam.	Bark	Percent Bark	Diam.	Bark	Percent Bark
1	21	8.8	6.5	7.4	8.4	3.8	4.5	7.2	3.5	4.9	5.5	2.4	4.4	4.8	1.9	4.0	4.1	1.9	4.6	3.2	1.8	5.6	1.5	1.6	10.7
2	21	5.3	4.5	8.5	3.8	1.8	4.7	3.1	1.4	4.5	2.2	1.2	5.5	1.3	1.0	7.7	0.6	1.0	16.7	....	...	...	....	...	....
3	30	11.0	5.5	5.0	9.5	5.0	4.5	8.0	3.8	4.7	7.0	2.5	3.6	6.3	2.5	4.0	4.8	2.3	4.7	4.0	2.0	5.0	....	...	....
4	33	11.0	6.5	5.9	10.5	6.0	5.7	9.0	4.5	5.0	8.0	4.8	5.9	6.0	2.3	3.8	4.8	1.8	3.7	3.3	1.3	3.5	2.5	1.5	6.0
5	30	4.5	4.5	10.0	4.0	2.0	5.0	3.3	1.5	4.6	2.0	1.0	5.0	....	...	...	....	...	....	....	...	...	....	...	....
6	24	4.5	3.0	11.1	3.8	2.5	6.7	2.5	1.5	6.0	2.0	1.8	8.8	....	...	...	....	...	....	....	...	...	....	...	....
7	37	10.5	6.0	5.7	10.0	4.0	4.0	9.0	3.5	3.8	8.5	4.0	4.7	5.5	2.0	3.6	4.5	2.0	4.4	....	...	...	....	...	....
8	54	15.5	8.0	5.2	15.5	8.0	5.2	13.0	6.5	5.0	13.0	6.5	5.0	10.5	4.5	4.3	10.0	4.5	4.5	7.0	3.0	4.3	6.0	2.8	4.6
9	21	5.5	3.0	5.5	4.5	2.0	4.4	4.0	1.8	4.4	3.8	1.0	2.7	2.5	1.0	4.0	....	...	....	....	...	...	....	...	....
10	30	10.0	5.0	5.0	9.0	3.8	4.2	8.5	3.8	4.4	7.5	3.0	4.0	6.0	2.5	4.2	4.5	2.0	4.4	....	...	...	....	...	....
11	...	20.5	13.0	6.3	19.0	7.0	3.7	16.5	7.0	4.2	15.0	7.5	5.0	15.0	7.0	4.7	14.0	7.0	5.0	12.0	6.0	5.0	11.0	6.0	5.5
Av.	30.1	9.7	5.9	6.1	8.9	4.2	4.7	7.6	3.5	4.6	6.8	3.2	4.7	6.4	2.7	4.3	5.9	2.8	4.7	5.9	2.8	4.7	5.3	2.9	5.5

Average growth in diameter per year = 0.29 cm.
Average annual bark increment = 0.17 mm.

TABLE XII

Data on *Acer rubrum*

Diameters are given in cm.; bark thicknesses in mm.

Tree no.	Age	Height of Measurement														
		Ground			1 meter			2 meters			3 meters			4 meters		
		Diam.	Bark	Per cent Bark	Diam.	Bark	Per cent Bark	Diam.	Bark	Per cent Bark	Diam.	Bark	Per cent Bark	Diam.	Bark	Per cent Bark
1	32	14.0	5.5	3.9	13.0	5.5	4.2	11.0	4.5	4.1	8.0	3.5	4.4	7.0	2.0	2.9
2	42	8.8	3.5	3.9	7.8	2.8	3.6	6.8	2.5	3.7	5.8	2.0	3.5	5.0	2.0	4.0
3	29	10.0	5.5	5.5	8.0	3.0	3.8	8.0	3.0	3.8	5.0	2.0	4.0	4.5	2.0	4.4
4	26	11.0	3.0	2.7	8.5	2.5	2.9	7.0	2.0	2.9	6.0	1.8	3.0	5.0	2.0	4.0
5	45	9.5	3.5	3.7	6.5	2.5	3.8	6.0	3.0	5.0	4.5	2.5	5.6	3.5	1.5	4.3
6	35	7.0	3.0	4.2	6.0	2.5	4.2	4.5	2.0	4.4	...	...	...	...	...	...
7	35	8.0	3.0	3.8	7.0	2.5	3.6	6.0	2.5	4.2	5.5	2.5	4.5	...	...	...
8	38	8.0	3.5	4.4	6.0	2.5	4.2	5.0	2.5	5.0	3.5	2.0	5.7	...	...	...
9	38	8.5	4.0	4.7	6.0	3.0	5.0	4.0	2.0	5.0	3.0	1.5	5.0	...	...	...
10	29	6.5	2.8	4.5	6.0	2.3	3.8	4.5	2.0	4.4	...	...	...	...	...	...
11	30	8.8	3.0	3.4	7.3	2.8	3.8	6.5	2.5	3.8	6.0	2.0	3.3	4.3	1.8	4.2
12	27	8.0	3.3	4.1	7.5	3.0	4.0	6.3	2.5	3.9	...	...	...	...	...	...
Averages	33.8	9.0	3.6	4.0	7.5	2.9	3.9	6.3	2.6	4.1	5.3	2.2	4.2	4.7	1.7	3.8

Average growth in diameter per year = 0.27 cm.
Average annual bark increment = 0.11 mm.

TABLE XII (*Continued*)

DATA ON *ACER RUBRUM*

Diameters are given in cm.; bark thicknesses in mm.

Tree no.	Age	Height of Measurement														
		5 meters			6 meters			7 meters			8 meters			9 meters		
		Diam.	Bark	Per cent Bark	Diam.	Bark	Per cent Bark	Diam.	Bark	Per cent Bark	Diam.	Bark	Per cent Bark	Diam.	Bark	Per cent Bark
1	32	5.5	1.8	3.3	5.0	1.5	3.0	3.5	1.3	3.7	2.0	1.0	5.0	1.1	0.5	4.5
2	42	3.5	1.5	4.3	...	...	...	...	...	...	...	...	...	...	...	...
3	29	3.5	1.5	4.3	2.3	1.0	4.4	1.0	0.8	8.0	...	...	...	...	...	...
4	26	4.0	1.5	4.3	3.0	1.3	4.3	...	...	...	...	...	...	...	...	...
5	45	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
6	35	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
7	35	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
8	38	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
9	38	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
10	29	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
11	30	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
12	27	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Averages	33.8	4.1	1.6	3.9	3.4	1.3	3.8	2.3	1.1	4.8	2.0	1.0	5.0	1.1	0.5	4.5

Average growth in diameter per year = 0.27 cm.
Average annual bark increment = 0.11 mm.

TABLE XIII

Data on *Quercus borealis*

Diameters are given in cm.; bark thicknesses in mm.

Tree no.	Age	Height of Measurement														
		Ground			1 meter			2 meters			3 meters			4 meters		
		Diam.	Bark	Per cent Bark	Diam.	Bark	Per cent Bark	Diam.	Bark	Per cent Bark	Diam.	Bark	Per cent Bark	Diam.	Bark	Per cent Bark
1	52	20.5	11.0	5.3	18.0	9.0	5.0	15.0	8.3	5.5	12.0	5.8	4.8	9.0	5.3	5.9
2	36	18.5	5.5	3.0	15.0	4.5	3.0	13.5	4.5	3.3	12.5	4.5	3.6	10.0	3.5	3.5
3	33	14.0	9.0	6.4	10.5	4.3	4.1	9.0	4.3	4.8	8.0	4.0	5.0	6.5	4.0	6.1
4	35	18.0	5.5	3.1	15.0	5.0	3.3	12.5	4.5	3.6	10.5	4.0	3.8	10.0	4.0	4.0
5	41	22.0	9.0	4.1	19.5	5.5	2.8	18.5	5.5	2.9	14.5	5.0	3.4	12.0	5.5	4.6
6	41	15.5	7.5	4.8	12.0	4.5	3.8	10.0	4.0	4.0	9.0	4.0	4.4	7.5	3.5	4.7
7	26	6.0	2.0	3.3	5.0	1.5	3.0	4.5	1.5	3.3	3.5	1.5	4.3	2.5	1.0	4.0
8	41	22.0	14.0	6.4	19.0	5.5	2.9	15.5	6.0	3.9	13.0	5.0	3.8	10.5	5.0	4.8
9	46	14.0	6.0	4.4	12.5	5.5	4.4	9.5	4.5	4.7	4.5	2.0	4.4	3.5	1.8	5.1
10	23	6.0	2.5	4.2	5.5	2.8	5.1	3.5	2.0	5.7	....	...	...	....	...	...
11	22	12.0	3.8	3.2	10.0	3.3	3.3	9.0	3.0	3.3	8.0	3.3	4.1	7.0	2.3	3.3
12	25	7.5	3.0	4.0	6.8	3.0	4.4	6.0	2.5	4.2	5.3	2.5	4.7	5.0	2.5	5.0
13	32	16.0	7.0	4.4	13.8	4.0	2.9	12.0	4.5	3.8	11.5	4.0	3.5	9.0	4.0	4.4
14	54	24.0	18.5	7.7	21.0	13.0	6.2	17.5	9.0	5.1	16.0	5.5	3.4	11.0	5.0	4.6
15	54	22.0	23.0	10.5	17.5	7.5	4.3	15.5	6.0	3.9	13.3	4.8	3.6	11.5	5.3	4.6
16	33	20.5	9.5	4.6	19.0	7.5	3.9	16.0	7.0	4.4	15.0	5.5	3.7	11.5	4.8	4.2
17	34	24.3	17.0	7.0	23.5	8.0	3.4	21.5	8.0	3.7	20.5	7.5	3.7	....	...	...
18	40	28.0	18.0	6.0	26.0	9.0	3.5	23.5	7.0	3.1	20.5	7.0	3.4	....	...	...
Averages	37.1	17.3	9.5	5.5	14.9	5.7	3.8	12.9	5.1	3.9	11.6	4.5	3.9	8.4	3.8	4.5

Average growth in diameter per year = 0.466 cm.
Average annual bark increment = 0.256 mm.

TABLE XIII (*Continued*)

DATA ON *QUERCUS BOREALIS*

Diameters are given in cm.; bark thicknesses in mm.

Tree no.	Age	Height of Measurement														
		5 meters			6 meters			7 meters			8 meters			9 meters		
		Diam.	Bark	Per cent Bark	Diam.	Bark	Per cent Bark	Diam.	Bark	Per cent Bark	Diam.	Bark	Per cent Bark	Diam.	Bark	Per cent Bark
1	52	7.5	3.5	4.7	5.8	3.3	5.7	4.3	2.5	5.8	...	...	...	...	...	...
2	36	8.5	3.5	4.1	6.5	3.0	4.6	5.0	2.5	5.0	...	...	...	...	...	...
3	33	5.0	3.0	6.0	3.0	2.0	6.7	2.5	1.5	6.0	1.5	1.3	8.7	0.8	0.5	6.3
4	35	8.5	4.0	4.7	7.0	3.5	5.0	6.0	3.0	5.0	4.0	2.0	5.0	2.5	2.0	8.0
5	41	10.5	4.5	4.3	7.5	3.5	4.7	5.0	2.5	5.0	...	...	...	...	...	...
6	41	5.5	3.0	5.4	3.0	2.0	6.7	...	...	...	...	...	...	...	...	...
7	26	1.5	0.8	4.3	0.5	0.5	10.0	...	...	...	...	...	...	...	...	...
8	41	8.0	4.0	5.0	6.0	3.5	5.8	...	...	...	...	...	...	...	...	...
9	46	....	...	...	...	...	....	...	...	...	...	...	...	...	...	...
10	23	....	...	...	...	...	....	...	...	...	...	...	...	...	...	...
11	22	3.5	2.0	5.7	...	...	....	...	...	...	...	...	...	...	...	...
12	25	4.0	2.0	5.0	...	...	....	...	...	...	...	...	...	...	...	...
13	32	8.5	3.5	4.1	6.0	3.0	5.0	4.5	2.8	6.1	...	...	...	...	...	...
14	54	8.8	4.3	4.9	6.0	3.0	5.0	4.0	2.5	6.2	...	...	...	...	...	...
15	54	8.5	4.8	5.6	6.0	4.0	6.7	...	...	...	...	...	...	...	...	...
16	33	8.5	4.8	5.6	6.5	4.0	6.2	4.5	2.5	5.5	...	...	...	...	...	...
17	34	....	...	...	...	...	....	...	...	...	...	...	...	...	...	...
18	40	....	...	...	...	...	....	...	...	...	...	...	...	...	...	...
Averages	37.1	6.9	3.4	4.9	5.3	2.9	5.5	4.5	2.5	5.6	2.7	1.7	6.3	1.7	1.3	7.6

Average growth in diameter per year = 0.466 cm.
Average annual bark increment = 0.256 mm.

The percentage relation of bark to diameter is highest in *Populus tremuloides*, 6.10, and next highest in *P. grandidentata*, 5.81; in the beech it is lowest, being 2.42. In comparison, the rubber trees of Matto Grosso, Brazil, showed a percentage of 1.22; 955 rubber trees in one plot in Sumatra, 2.26. The highest correlation between bark thickness and diameter found in these studies was that for *Betula lutea*, + 0.796; that for *Tsuga canadensis* was + 0.689; and that for *Populus grandidentata*, + 0.499. The correlation between bark thickness and circumference of tree for 955 Hevea trees in Sumatra was + 0.26 (5). No correlations between bark and diameter, or between bark and circumference, are known for any other species.

The rate of bark growth in Michigan trees is remarkably low. The rate for *Quercus borealis* is 0.256 mm. yearly; for *Populus grandifolia*, 0.215 mm.; for *P. tremuloides*, 0.174 mm.; and for *Acer rubrum*, 0.107 mm. The writer (4) found that 472 Hevea seedlings, one and one-half years old, had produced an average of 0.85 mm. of bark per year; and 126 seedlings of Hevea two and one-half years old had a mean annual bark growth of 1.13 mm. A plot of 1,000 nine-year-old Hevea trees showed a mean annual bark increment of 1.07 mm.; and Hevea bark which had been removed in tapping was regenerated at the rate of 1.93 mm. per year. The rubber tree undoubtedly has remarkable powers of regeneration, but whether the original growth of bark is unusually rapid is not known. Data on other tropical trees are lacking. Possibly, when more information is secured, we may find that in rate of bark production temperate trees do not compare so unfavorably with tropical trees as would appear from these figures.

The very slow growth of bark in our trees shows that the layer of phloëm which is produced yearly must be very small. This layer is usually a relatively small portion of the bark; therefore either the phloëm must remain functional for a number of years, or the amount serving the tree at a given time must be very small. Further investigation of this point may shed light on the question whether or not the quantity of phloëm is adequate to perform the function commonly assigned to it.

The study of the relation between bark thickness and diameter at different heights in the tree shows that the bark thickness decreases rapidly from the ground to a height of one meter, and more slowly from one meter upward. The diameter decreases at a uniform rate from the ground upward. The percentage relation between bark and diameter decreases rapidly between the ground and the one-meter level, and increases again in the upper levels of the trunk, becoming in some instances greater at the top of the trees than at the ground level. This greater percentage at the top may be owing to an irreducible minimum of bark, which must be present on even a small stem. Cursory examination indicates that the percentage relation of bark to diameter is greater in small trees than in larger ones, perhaps because the small trees have only the needed minimum of bark.

It appears that trees which taper rapidly have a greater variation in the relation of bark to diameter than those with boles which thin down more slowly. The writer (3) has found something of this condition in *Hevea brasiliensis*, in which the bark of trees with conical trunks decreases much more rapidly from the ground upward than in those with cylindrical trunks.

SUMMARY

1. Measurements of bark thickness were made on *Tsuga canadensis*, *Betula lutea*, *Acer saccharum*, *Acer rubrum*, *Populus grandidentata*, *Populus tremuloides*, *Fagus grandifolia*, and *Quercus borealis*.

2. *Tsuga canadensis* has the thickest bark of all Michigan trees; *Fagus grandifolia*, the thinnest bark of all large trees of the region.

3. The percentage of bark relative to diameter of trunk is greatest in *Populus tremuloides* and least in *Fagus grandifolia*.

4. The coefficient of correlation between bark thickness and diameter for *Betula lutea* is + 0.796; for *Tsuga canadensis*, + 0.689; and for *Populus grandidentata*, + 0.499.

5. *Quercus borealis* showed a mean annual bark increment of 0.256 mm.; *Populus grandifolia*, 0.215 mm.; *Populus tremuloides*, 0.174 mm.; and *Acer rubrum*, 0.107 mm.

6. The relation between bark thickness and diameter at different heights of the tree was investigated in four species.

7. The percentage of bark relative to diameter decreases rapidly from the ground level to a height of one meter, and increases again near the top of the tree.

University of Michigan

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HYSTERIACEAE: LIFE-HISTORIES OF CERTAIN SPECIES *

MARION LEE LOHMAN

THE writer has undertaken to determine by pure-culture methods the status of stages in the life-histories of species of the Hysteriaceae, a family of doubtful affinities, composed largely of species seldom reported and poorly understood. Collecting was begun in the summer and fall of 1928.

HISTORICAL

Species studied in culture

If one regards the genus Hysterium as typical for these fungi, as Von Höhnel (19) did, then the only culture studies that are known with any certainty for these forms are those of Brefeld (3, p. 271) with "*Glonium lineare* (Fr.), *Hysterium pulicare* (Pers.), *Hysterographium biforme* (Fr.), . . . *Lophium mytilinum* (Pers.), *Hysterographium Fraxini* (Pers.) . . . ." Concerning these species Brefeld states that all except the last yielded in culture a luxuriant, widespread, brown or gray mycelium, and that none produced any sign of fructification during the nine or ten months of observed growth. *H. Fraxini* produced a very scant growth of white mycelium. According to Brefeld (2), Möller studied *H. pulicare* in culture and obtained similar mycelia from germinating "spermatia" and ascospores.

Taxonomy

The order Hysteriales, as commonly delimited, is equivalent to the Hysteriineae of Lindau (27), who retained the terminology of Schroeter (42, pp. 62, 142), described the group, and subdivided it into five families, with a total of twenty-nine genera. At a later date he (28) added five more genera. This classification

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is fundamentally the same as that proposed by Rehm (36). In contrast to these systems we have Saccardo's Hysteriaceae (*Syll. Fung.*, 2 : 721. 1883) with twenty-eight genera at first, a number later increased to fifty-three through additions in subsequent volumes of the *Sylloge Fungorum.*

Bisby (1) has well reviewed the early literature on the taxonomy of the group and has also summarized Von Höhnel's disposition of the genera of Saccardo's Hysteriaceae.[1] The studies of Hilitzer (18), Lagerberg (24), Lind (26), Minks (32) and Rehm (38), and the ideas expressed by Fink (14–16) on the classification of these fungi might be added — largely for their historical interest — to supplement the review by Bisby. Hilitzer's recent monograph presents named and described pycnidial stages for a number of the species of the Hypodermataceae and for six species of the Hysteriaceae. The author proposed the form genus Hysteropycnis to receive the latter. The paper of Lagerberg contains in part a discussion on the limitation of genera in the Hypodermataceae.

As early as 1881 Minks set about to establish a line of demarcation between lichens and hysteriaceous fungi, placing greatest emphasis on hymenial structure. Although he made no definite disposition of species, suggesting that this might be done by the various systematists on the basis of his notes, it is apparent that he favored the transfer of many carbonaceous, hysteriaceous forms to the category of lichens. Rehm, again revising the Hysteriineae in 1912, transferred his genus Hysteropatella from the Patellariaceae to this family. Fink, in distributing lichen genera among the Fungi, placed the Graphidaceae and the Arthoniaceae in the Hysteriales.

The Hysteriaceae as limited by Von Höhnel (19) include 327 described species. Approximately 100 have been reported for North America, and of that number 81 have been described,

[1] In a later paper, "Type Specimens of Certain Hysteriales," Professor G. R. Bisby has summarized his notes on certain types in European herbaria. His paper is a recent, significant advance in the status of the nomenclature in these fungi. I am thankful to him for the privilege of examining a copy of his manuscript while his paper was in press. It has since been published in *Mycologia*, 24 : 304–329. 1932.

largely by early workers, from American material. It is estimated that about 60 per cent of the species described from American material have not been reported since the original discovery, or that collections have been questionably referred to such species. This situation results from our ignorance of diagnostic characters and specific limitations in these fungi, and suggests that any satisfactory revision of this family must await comparative culture studies.

Associated conidial stages

In 1897 Lindau (27, p. 266) summarized the status of imperfect stage connections in the Hysteriales somewhat as follows: "So far as known the members of the Hysteriales do not produce imperfect stages in culture, but only sterile mycelia. Pycnidia have been observed as associated with many species. These are in part Leptostromaceae (Hypodermataceae) and in part Excipulaceae (species of Dichaena). The conidia are always elongate, unicellular, and hyaline." It is to be noted that none of the species of his Hysteriaceae are included. As a matter of fact, associated imperfect stages had been described in the literature previous to 1897, for several species of Hysterium, for *Hysterographium Fraxini*, and for two species of Lophium. However, only the conidial stages of the two species of Lophium were referred to definite form genera at that time.

A review of the literature on hysteriaceous species indicates that even brief descriptions of associated imperfect stages exist for only a few species. Some of these associations are very questionable and none have been demonstrated by cultural methods.

Dichaena. — The exact status of the species that have been referred to the genus Dichaena (Fries, *Sys. Orb. Veg.* 1 : 108. 1825) is not clear. It is commonly stated that the conidial stage of these species appears as a stylosporic fructification within the hysterothecium and that the ascigerous stage is seldom produced. Descriptions of imperfect stages (Psilospora and Dichaenopsis) that have been referred to the several species are also conflicting.

Gloniopsis. — Hilitzer (18) described *Hysteropycnis admixta* Hilitzer as a pycnidial stage in association with a form which has been known as *Gloniopsis biformis* (Fr.) Sacc. He contended

that the perfect stage is not referable to *Hysterium biforme* Fr. and, not giving Gloniopsis generic ranking, proposed the name *Hysterographium Dubyi* Hilitzer. The pycnidia of this fungus are globular, 0.1–0.3 mm. in diameter, and the pycnidiospores are hyaline, elliptic, and measure 3–5 × 1–1.5 μ.

Glonium. — *Hysteropycnis globularis* Hilitzer (*op. cit.*, p. 151) is described as a pycnidial stage associated with *G. lineare* (Fr.) De Not. (*Psiloglonium lineare* Petrak). The pycnidiospores are elliptic or elliptic-oblong and measure 4–5 × 1.5–2 μ.

Hysterium. — Brefeld (2, p. 47) mentioned that Möller had germinated the conidia from fructifications associated with *H. pulicare* (Pers.) Fr. No description is given. In the description of *H. Prostii* Duby, Saccardo (*Syll. Fung.*, 2 : 746) described the conidia as elongate and stalked. Duby (9, p. 38) did not mention the conidia when he described the species. Saccardo (*op. cit.*, 2 : 716) described the conidia of *H. melaleucae* F. Tassi as hyaline and stalked, measuring 2–2.5 × 0.3–0.5 μ. Hilitzer (18, p. 151) described a pycnidial stage for *H. alneum* Schröt. (*H. pulicare*) and named it *Hysteropycnis occulta.* The pycnidia measure 0.05–0.1 mm. in diameter, and the pycnidiospores are simple, elliptic, hyaline, and measure 2–3 × 0.5–1 μ.

Hysterographium. — Rostrup (40) described a pathologic condition of young ash and concluded, without inoculation or other cultural studies, that *H. Fraxini* (Pers. ex Fr.) De Not. was the causal organism. On the diseased ash a pycnidial stage with hyaline, cylindrical, stylosporic conidia measuring 32–38 × 11 μ appeared in the summer and later, on the same areas but particularly on the fallen twigs, the hysterothecia of *H. Fraxini* were produced. He associated the pycnidial stage with the long-known perfect stage. Rostrup indicated in a later publication (41, p. 120) that he had observed this organism as a parasite of the ash in several other localities. Lind (26) referred the pycnidial stage to the form genus Myxosporium.

Hilitzer (18, p. 152) described a pycnidial stage for *H. Fraxini* as *Hysteropycnis Fraxini.* The pycnidiospores are cylindric, hyaline, and measure 3–6 × 1–1.5 μ. He also described *Hysteropycnis confluens*, with pycnidia measuring 0.1–0.5 mm. in diameter,

and with hyaline, oblong-elliptic pycnidiospores measuring 3–4.5 × 0.5–0.8 μ, as an imperfect stage associated with *Hysterographium elongatum* Corda.

Lophium. — The Tulasnes (*Sel. Fung. Carp.*, 2 : 259) considered *Phragmotrichum Chailletii* Kunze & Schmidt (Kunze, *Myk. Hefte*, 2 [1823] : 84, t. 2, f. 4; Engler and Prantl, *Natür. Pflanzenf.*, 1, Abt. I [1899] : 414, f. 216, D) to be a conidial stage of *L. mytilinum* (Pers.) Fr.

According to Rehm (36, p. 1211), *L. Eriophori* Hennings is accompanied by *Leptostroma Henningsii* Allescher. The elongate, hyaline, unicellular conidia measure 5–8 × 1 μ. In 1912 Rehm remarked (38, p. 112) that *L. Eriophori* might be nothing more than a form of *L. mytilinum*. This is the only association in which a Leptostroma connection has been suggested for a hysteriaceous fungus.

Mytilidion. — Duby (9, p. 27) described the spermatia as "free" for *M. aggregatum* (DC.) Duby. In the generic description (*op. cit.*, p. 34) he stated that the spermatia were minute, elliptic-elongate, hyaline, and produced in mucilaginous layers in the membranous spermatogonia. Rehm (35), in his revision of the Hysteriineae in the herbarium of Duby, noted for one of the specimens (*Lophium aggregatum* Fr.) under the name given above that the spermatia were hyaline, mostly curved, and measured 5 × 1 μ. In connection with *M. aggregatum* Duby, Hilitzer (18) mentioned globular, ostiolate pycnidia 0.1 to 0.2 mm. in diameter, with pycnidiospores 2 to 2.5 μ in diameter.

The writer's announcement (30) that he had obtained a pycnidial stage of the Sphaeronaema type in pure cultures of *Glonium parvulum* (Ger.) [Sacc.] Cke. is apparently the first one that establishes definitely an imperfect stage connection in the hysteriaceous fungi.

METHODS AND MATERIALS

Isolations

The stock cultures used in this study originated in the isolation of single germinating ascospores and individual asci with retained germinating spores, from sprays on Kauffman's synthetic agar

medium. The recipe for preparing this medium, the method of isolation, and the succession of physical factors to which stock cultures were subject have been published by the writer (30, pp. 144, 146). The colored and comparatively large spores in most of the species, and the fact that conidial stages upon or within the hysterothecium are not common, made single-spore isolation a relatively easy task.

Ascospore germination

The physiological state of maturity of a spore determines the exact stimuli which will affect its germination, and when both are known, spores can be germinated at will. But in these slowly growing fungi the maturity of a given spore sample from collected material is not definitely determinable. To ascertain the effects of the season on maturity, groups of undisturbed hysterothecia of *Glonium parvulum*, *Hysterographium Mori*, and *Gloniopsis Gerardiana*, on their natural substrata, were subjected to natural weathering through two winters and the intervening warmer months, and were examined at intervals. Throughout the period of observation no noticeable changes occurred in the apparent maturity of hysterothecia, and microscopic examinations always revealed hymenial elements of varying development. Several of the species have been collected in "good condition" during all seasons of the year. It is evident that the hysterothecia are perennial and that the plants continue to produce and mature their spores for at least a few years within a single fruit body. In the examination of material it is not uncommon to find spores that have germinated within the ascus. Yet in some species, *Hysterographium vulvatum* and *H. Fraxini* in particular, ascospore germination proved to be a real problem.

The stimulus employed to induce spore germination in certain collections was a periodic wetting and drying at room temperature at intervals of from twelve to forty-eight hours for several days. Such treatment failed to stimulate germination in *H. Fraxini*. After being subjected to freezing temperatures (− 30, − 25, or − 4° C.), with intervals of thawing at 25° C., spores at various stages of morphological maturity germinated readily.

Since the Hysteriaceae present spores of widely diverse morphological types, and since the present genera are delimited largely by spore characteristics, the comparative morphology of the germ-tube hyphae was studied in particular. The results and the conditions under which germination was observed are presented elsewhere (31).

The germination of secondary spores

Hyphomycetous and sphaeropsidaceous imperfect stages have been encountered in the study of these fungi. The terminology would be more in accord with that of past literature if the latter types were referred to as spermatogonia, since the fructifications are very minute and their spores are extremely small, hyaline, and unicellular. However, these so-called spermatia have been germinated in nearly half of the species studied, and it is appropriate that the fructifications be referred to as pycnidia, and their reproductive cells as pycnidiospores. Moreover, in *Lophium mytilinum*, *Glonium parvulum*, and *Hysterium insidens* single-pycnidiospore isolations have yielded mycelia vegetatively indistinguishable from the single-ascospore cultures of the same species. A culture derived from a single, culturally produced pycnidiospore is illustrated (Fig. 31*A*).

The method of alternate wetting and drying stimulated pycnidiospore germination. It usually had to be employed in the germination of culturally produced pycnidiospores. After a prolonged treatment of the pycnidiospores from field material the writer succeeded in germinating them in *Lophium mytilinum*, but failed in *Glonium stellatum*. In the attempt to isolate the latter species, and in the isolation of *Lophium mytilinum* and *Hysterium insidens* from secondary spores obtained from field material, the procedure outlined for the isolation of ascospores was followed, except that it was necessary to omit the initial washing in 95 per cent alcohol. The germination of secondary spores was observed in distilled water and, for species isolated from such spores, on nutrient agar plates. Tests for germination were made at 20 to 25° C.

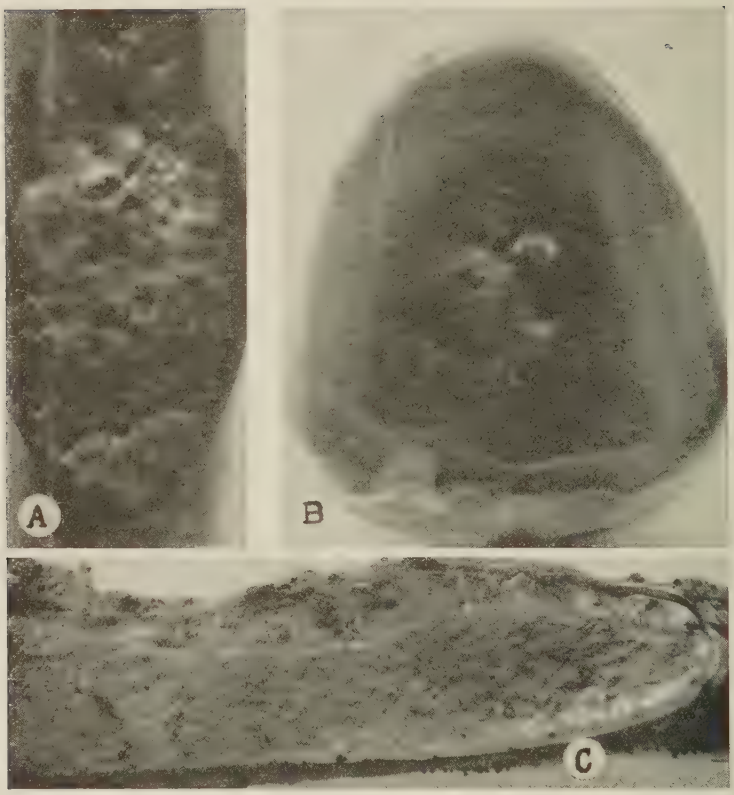

FIG. 31. *A*, *Glonium parvulum.* Mature pycnidia (*Sphaeronaema parvulum*) twice the actual size, with their apical globular masses of exuded spores; single-pycnidiospore culture on the Leonian medium after eleven months at 20 to 25° C. *B*, *Hysterium insidens.* Massed conidial (*Septonema spilomeum*) filaments, actual size; single-ascus culture on the Leonian medium after four months at 20 to 25° C. *C*, *Lophium mytilinum.* Erumpent, composite, pycnidial fructifications twice the actual size; single-ascospore culture on pine bark seated in a pine-bark decoction agar medium; seven months at 20 to 25° C.

Culture media

Stock cultures were maintained on a sucrose-oatmeal medium containing 60 gr. of ground oatmeal, 40 gr. of cane sugar, and 15 gr. of agar to one liter of distilled water. Leonian's agar (25, p. 21), peptone omitted, was adopted as a medium favorable to the production of imperfect stages. Comparative culture notes on vegetative habits were recorded for cultures on these two media, although the former can scarcely be considered a standardized medium. Special substrata, such as sterilized Quercus and Prunus blocks, Rhus and Fraxinus twigs, Pinus bark and mixed-wood sawdust, were utilized in the culture of certain species. These are indicated in the discussion of the particular species. Species from coniferous hosts were cultured on a 2 per cent agar medium of pine-bark decoction.

Fungi in culture

The following species were grown in culture: *Lophium mytilinum* (Pers.) Fr., *L. dolabriforme* Wallr., *Glonium stellatum* Muhl. ex Fr., *G. simulans* Ger., *G. parvulum* (Ger.) Cooke, *G. lineare* (Fr.) De Not., *Mytilidion tortile* (Schw.) Sacc., *M. laeviusculum* (Karst.) Sacc., *M. decipiens* (Karst.) Sacc., *M. resinicola*, sp. nov., *M. Thujarum* (C. & P.), comb. nov., *Hysterium pulicare* Pers. ex Fr., *H. angustatum* Alb. & Schw., *H. insidens* Schw., *Hysterographium kansense* E. & E., *H. minutum*, sp. nov., *H. Mori* (Schw.) Rehm, *H. Lesquereuxii* (Duby) Sacc., *H. formosum* (Cooke) Sacc., *H. vulvatum* (Schw.) Rehm, *H. Fraxini* (Pers. ex Fr.) De Not., *Gloniopsis brevisaccata*, sp. nov., *G. Gerardiana* Sacc., *Hysteropatella Prostii* (Duby) Rehm, and *H. clavispora* (Peck) Seaver.

LIFE-HISTORIES [2]

Lophium mytilinum (Pers.) Fr.

No. 191. Fruiting abundantly on bark and exposed wood of dead branches of *Pinus sylvestris* L., Ann Arbor, Mich., Nov. 5,

[2] The collections upon which the studies are based are deposited in the University of Michigan Herbarium. Their numbers, as indicated herein, represent both the writer's culture number and the accession number in his herbarium. In the notes treating general cultural characteristics reference

1929. Collected by G. B. Cummins and M. L. Lohman. No. 280. On twigs of *Pinus Strobus* L., Ann Arbor, Mich., Sept. 19, 1930. Collected by M. L. Lohman.

Mature hysterothecia, 0.4–0.7 × 0.1–0.5 mm., the height equaling or exceeding the width; asci 150–190 × 7–8 μ; spores (120) 140–175 × 2 μ, yellowish hyaline, filiform, and 18–20-septate.

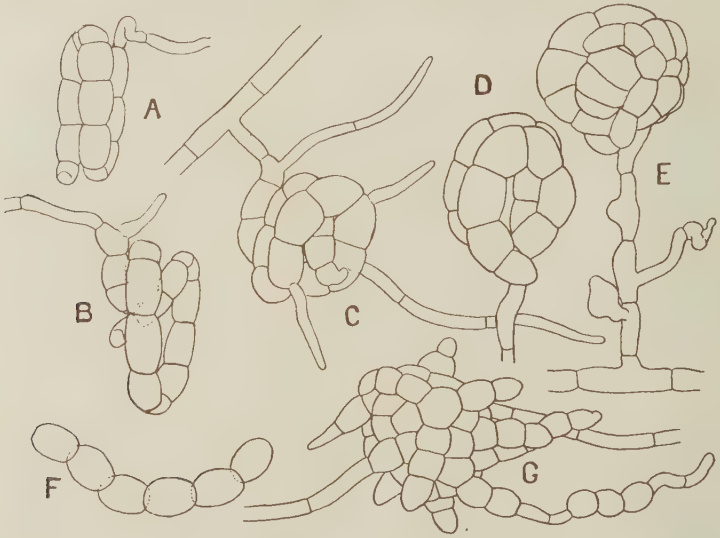

FIG. 32. *A–E, Lophium mytilinum; Papulospora mytilina* stage. *A–B*, early stages in conidial development; *C*, a germinating conidium; all from cultures. *D–E*, conidia from field material. *F–G, Lophium dolabriforme. F*, portion of catenulate filament from superficial layer in cultures; *G*, sclerotial body from surface layer in cultures

L. mytilinum has also been collected near Ann Arbor, on cones of *P. ponderosa* Dougl. and on old stumps of *Larix laricina* (Du Roi) Koch.

Vegetative cultural characteristics. — Growing mycelia are dark ("dark grayish olive" to "olivaceous black 2"), with a lighter

is to cultures on the Leonian and oatmeal media in the light at 20 to 25° C., unless other conditions are recorded. Quoted color terms are those of Ridgway (39).

greenish tinge at the margin. The aërial hyphae are lighter in color and soon become "light pinkish cinnamon" to "wood brown." The species produces a pink coloration of the oatmeal medium, especially in cultures held at the lower temperatures. A hyphomycetous stage (Figs. 32 *A–E*) and a pycnidial stage (Fig. 33) have been obtained on single-ascospore, single-ascus,

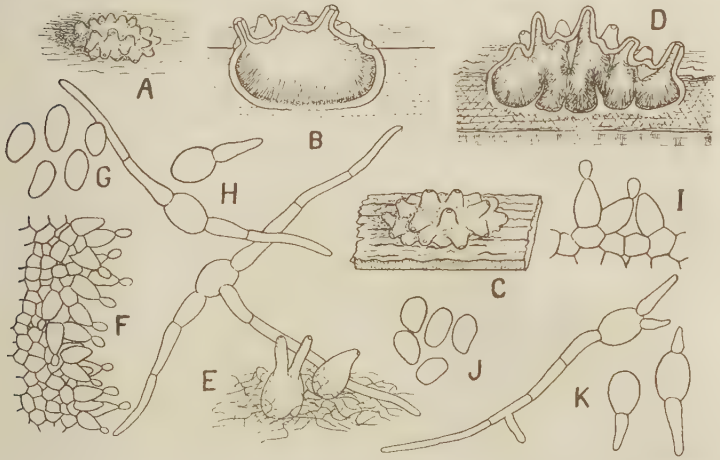

Fig. 33. *Lophium mytilinum;* pycnidial stage. *A*, a pycnidial fructification on agar medium, × 30; *B*, the same in sectional view; *C*, a pycnidial fructification in outer bark of *Pinus strobus* twig, × 60; *D*, the same in sectional view; *E*, pycnidia from the superficial layer in cultures on mixed-wood sawdust; *F–G*, spore-bearing cells and spores from *C*; *H*, germinating pycnidiospores from field material; *I–J*, spore-bearing cells and spores from *A*; *K*, germinating pycnidiospores from fructifications obtained in culture

single-conidium, and single-pycnidiospore cultures grown on various media.

Cultural fructifications. — Anastomosing aërial hyphae initiate "bulbil" primordia, each of which may develop one or several subglobose, dark fuscous, propagative bodies (herein referred to as conidia) of the Papulospora type (Figs. 32 *A–B*). The conidia develop as coiling-hyphal tips which form spirals of several turns each. The coiling hyphae are closely septate, and the distal

ends of many grow tortuously through the coils to form compact conidia measuring 15 18 × 10–12 μ, the smaller dimension being in the direction of the axis. The coiling hypha is 3 to 5 μ in diameter and seldom branches in the formation of a single conidium. Additional conidia arise either by the prolongation of the conidiophore or by the development of a secondary conidiophore from the first or second cell of the coil. These processes in some specimens are continued until six or eight conidia are formed in close proximity. Occasionally compound bulbils result wherein single conidia are not discernible. The spiral condition is not always evident in a mature conidium. On the oatmeal medium at 10° C. these conidia were not produced, but, instead, torulose hyphae developed numerous, clustered, septate, uncoiled, tortuous, finger-like projections, undoubtedly potential conidial filaments, because mature conidia were obtained on this medium at higher temperatures. Typical conidia were obtained on the Leonian medium at 10° C.

The conidia obtained in culture were isolated, their germination was studied, and single-conidium cultures returned the conidial stage and produced a pycnidial stage as well.

Single-ascospore and single-ascus cultures on the Leonian medium produced a pycnidial stage on their marginal mycelia within five to eight weeks. The black, erumpent fructifications were carbonaceous, at first smooth above but later ten to twenty-four ostiolate-papillate (Figs. 33 *A–B*). Exuding pycnidiospores collected in gelatinous spherical masses at the tips of the minute papillate tubercles. In general, the compound pycnidia obtained on agar media measure (250) 400–600 × (200) 350–400 μ. They have complete, subcarbonaceous, parenchymatous walls 10 to 15 (20) μ in thickness, with the outer cell layers opaque, the inner hyaline, and bearing sporulating cells. The ostiolate papillae vary greatly in length. They measure 30 to 40 (60) μ in their median diameter. The sporulating cells are obovate, (2.5) 3–5 × 2 2.5 μ, and they line the lateral and basal walls and abstrict the pycnidiospores singly from their tips. The pycnidiospores are hyaline, oblong-elliptic to inequilateral or suballantoid, and they measure 1.5–2 (2.5) × 1–1.5 μ. They germinate, after con-

siderable swelling, by one or two terminal germ hyphae (Fig. 33 *K*). At maturity the compound fructification is provided with a single cavity and a number of papillae.

Cultures on sterilized deciduous-wood sawdust produced pycnidia in the aërial mycelium, a circumstance which Coons (5) attributed to unfavorable physico-chemical conditions. These pycnidia (Fig. 33 *E*) were smaller, measuring (75) 100–150 × (95) 130–150 μ exclusive of the beaks. The latter measured (120) 140–170 μ in length, with an average median diameter of 25 to 30 μ. A number of the smaller pycnidia possessed but one beak. In these cultures the young pycnidia are globose and at first develop outwardly in all directions by the close interweaving of minute, tortuous hyphae. Later a central cavity appears, development is upward, and the beaks appear as pycnidiospore formation is initiated. In the aërial mycelium the primordia arise symphogenously, a manner of pycnidial development considered by Kempton (23) to be uncommon.

Observed associations. — The first collections of *L. mytilinum* exhibited an associated hyphomycetous stage, which was questionably referred at the time to *Helicoma olivaceum* (Karst.) Linder (29, p. 302). When less symmetrical conidia appeared in cultures of *L. mytilinum*, numerous collections of the perfect stage were made to determine the constancy of the conidial form in the associated hyphomycetous stage, particularly since Linder, basing his opinions on culture studies, has emphasized the constancy of spore form in species of helicosporous fungi. Further studies disclosed the fact that the first collections were only early stages in the development of a Papulospora type of conidium similar to that obtained in culture.

The conidial stage is most abundant on the wood or inner bark beneath the loosened outer bark. On exposed surfaces the conidia are readily disseminated, and only a dark brown hyphal crust remains. It is not uncommon to find this crust crowning old pycnidial clusters on dead twigs. When in good condition the conidial clusters completely fill the cavities left by the disintegrated pycnidia. In the less exposed areas the conidia are produced in irregularly circular clusters 100 to 200 μ in diameter.

They are closely compact, olivaceous to brown in mass, but become black on drying. In the first-coil stage they are five- to seven-celled and measure 13–15 × 8–10 μ. At maturity they are compactly and rather indistinctly coiled, and are 16–18 (24) × 13–15 μ. The yellowish conidiophores are two- to four-celled, 15 to 30 μ in length, and 2.5 μ in diameter, or, in proliferating clusters, they are scarcely discernible. Widely effused brown crusts formed by compact, upright, branching, torulose, non-sporiferous hyphae 45 to 50 μ in length and 5 μ in diameter are not uncommon. No stage has been observed comparable to *Phragmotrichum Chailletii* Kunze & Schmidt (see p. 233), which is recorded in the literature as an imperfect stage of *L. mytilinum*.

Conidial development in this hyphomycetous stage is the same as that described by Hotson (21, p. 283) for *Papulospora sporotrichoides* Hotson, and in his artificial classification the stage would occupy a similar position. However, in the stage described above, the mycelium is dark, the bulbils are smaller, and the accessory conidia are produced in pycnidia. The name **Papulospora mytilina** (Pers.) Lohman, status novus *Lophii mytilini* (*Hysterium mytilinum* Pers., *Syn. Meth. Fung.*, p. 97. 1801) is suggested.

The pycnidial stage obtained in culture has not been found on *Pinus sylvestris*, but a small collection was obtained from recently dead, attached twigs of *P. Strobus*. The black pycnidial clusters (Figs. 33 *C–D*) are intracorticular, with erumpent ostiolate papillae. They measure 250 to 300 (400) μ in diameter and 200 to 250 μ in height. The number of papillae to each fructification ranges from one to fifteen, with an average of eight to twelve. The papillae average 30 μ in the median diameter and are scarcely as high as broad. At maturity a fructification may have a single conidial cavity common to all the papillae or, if in the development of the fructification the coalescence of cavities has not been completed, several cavities may be apparent. The wall of the fructification is complete, subcarbonaceous, 10 to 15 (20) μ thick, and is parenchymatous with four or five to eight or ten cell layers, the outer cells opaque, and the inner, hyaline and sporogenous. The spore-bearing cells are globular to obovate, 3–4 (5) × 2–3 μ,

although occasionally more elongate, and they abstrict the pycnidiospores singly. The spores are hyaline, acrogenetic, ovate-inequaliteral to suballantoid, and measure 2–2.4 × 1–1.3 μ. Single-pycnidiospore cultures from this material produced mycelia identical with those of single-ascospore cultures. After three months several of such cultures on the Leonian medium had produced the Papulospora stage, but only one culture on oatmeal agar had returned the pycnidial stage.

A pycnidial fructification of the foregoing description shows certain characters of the form genus Dothiorella, but differs from it in the development of a single cavity at maturity.

Lophium dolabriforme Wallr.

No. 196. On dead twigs on shrub, *Salix sp.*, at 9,000 ft., north of Grand Lake, Colo., Aug. 27, 1928. Collected by M. L. Lohman.

Hysterothecia 0.75 to 1.5 mm. in height, 0.5 to 0.7 mm. in length, black, carbonaceous, fragile, ligulate with the typical corrugations, and mostly free from the substratum except for the brown, rhizoidal, hyphal strands; asci 300–360 × 8–10 μ; spores in young asci nearly as long as the ascus, but at maturity fragmenting into sections averaging 12 × 2 μ, at first yellow and 1-septate, then yellow-brown and 3-septate.

The best description of the European fructifications has been given by Rehm (36, p. 27). A comparison of his measurements of the hysterothecia with those given by Ellis (11, p. 124) and with those of the Colorado material indicates that the American form is considerably smaller.

Vegetative cultural characteristics. — All cultures of this species showed extremely slow growth (Table I). Marginal hyphae are dark, slightly immersed, sparingly branched, and grow radially outward in a straight course with the branches arising at an acute angle and growing immediately outward in parallel courses. The hyphae of rhizoidal strands and of the prosenchymatous tissue of the fruiting structures in collected material suggest this manner of growth. On agar media the organism produces a loose, prosenchymatous surface weft several millimeters in depth. A gray

TABLE I

Approximate Radial Growth Attainments, Relative to Temperature, on Oatmeal Medium at the End of Eight Weeks

10° C.			Species	22–25° C.		
75 mm.	50 mm.	25 mm.	0	0	25 mm.	50 mm.	75 mm.
			LOPHIUM				
-	-----	-----	L. mytilinum	-----	-----	--	
		---	L. dolabriforme	-			
			GLONIUM				
-	-----	-----	G. stellatum	-----	-----	-----	
	----	-----	G. simulans	-----	-----	--	
		-----	G. parvulum	-----	-----		
		-----	G. lineare	-----	---		
			MYTILIDION				
	-	-----	M. tortile	-----	---		
	--	-----	M. laeviusculum	-----	-----	--	
		-----	M. decipiens	-----	--		
	-	-----	M. resinicola	-----	-----		
		-----	M. Thujarum	-----	---		
			HYSTERIUM				
		---	H. pulicare	-----	---		
		----	H. angustatum	-----			
		---	H. insidens	----			
			HYSTEROGRAPHIUM				
		----	H. kansense	-----			
	---	-----	H. minutum	-----	-----	---	
		-----	H. Mori	-----	-----	-	
	-	-----	H. Lesquereuxii	-----	-----	-	
	-----	-----	H. formosum	*			
		---	H. vulvatum	----			
	--	-----	H. Fraxini	-----	---		
			GLONIOPSIS				
	--	-----	G. brevisaccata	-----	-----	--	
		-----	G. Gerardiana	-----	--		
			HYSTEROPATELLA				
		---	H. Prostii	-----	---		
		---	H. clavispora	-----	---		

* No radial increase, but cultures remained viable; sclerotic development.

("light mouse gray," becoming "olive-brown" to "hair brown") aërial mycelium is loosely interwoven and averages one millimeter in depth. Microscopically, the twisted, sparingly branched hyphae of this mycelium are close-septate, torulose to catenulate, yellow-brown, and measure 3 to 4 μ in diameter. Similar torulose hyphae (Fig. 32 *F*) arise as black, semisuperficial clusters on the marginal mycelia of old cultures arrested in growth. If one considers the individual cells as conidia, then one is here concerned with conidial chains which do not fragment readily and which possibly conform to the dematiaceous Gyroceras type. The surface of an old culture becomes covered with these filaments and the culture appears darker ("blackish mouse gray") than described above.

Sclerotial bodies (Fig. 32 *G*) 10 to 20 μ in diameter are common on the surface of oatmeal cultures. Neither the catenulate filaments nor the sclerotial bodies are associated with the writer's collected material, but it is scant. If sclerotia are produced in the field they would probably precede the perfect stage and, if superficial, would disappear early.

In this report this is the only species in which a tissue culture has been given consideration. The ascospores did not germinate; stock cultures carried originated in the rejuvenescence of hyphae of the rhizoidal strands. However, the rarity of the organism warrants inclusion of these brief culture notes, which can stand only as circumstantial evidence until the fungus is grown from single-spore isolations.

Glonium stellatum Muhl. ex Fries

No. 195. At base of old stump, Boston, Mass., March 26, 1927. Collected by Dr. L. E. Wehmeyer. No. 265. On much-decayed Quercus log, Livingston County, Mich., Aug. 13, 1930. Collected by M. L. Lohman.

Asci 70–90 × 8–9 μ; spores (20) 22–24 (27) × (4.5) 5–6 μ, hyaline, 2-celled, elliptic-fusiform, slightly curved with acuminate ends.

G. stellatum Muhl. ex Fries is considered the type of the genus which Muhlenberg proposed in 1813 (*Cat. Pl. Am. Sept.*,

p. 101). De Notaris (6), the first person to amend the old generic description to include species with simple hysterothecia not seated upon a byssoid subiculum, placed emphasis on spore characteristics. He argued (*op. cit.*, p. 25) that *G. stellatum* is atypical for the forms with 2-celled hyaline spores. It was in consideration of these same points that Von Höhnel (19) erected the subgenus Psiloglonium, and that Petrak (34), in connection with additional characters of questionable value, raised Psiloglonium v. H. to generic rank, retaining it in the Hysteriaceae, and intimated that *G. stellatum* Muhl. and other species exhibiting a byssoid subiculum are much out of place in Von Höhnel's family. Petrak described the spores of *G. stellatum* as two-celled or more.

Those who have reported the spores to be more than 1-septate have undoubtedly observed spores that were in an arrested early stage of germination. Germinating spores of the four species of Glonium presented here have been compared and figured by the writer (31).

Vegetative cultural characteristics. — Vigorous mycelia are a blue-black ("plumbeous black" or "dusky purplish gray"). The fungus produces a "dark violet gray" coloration of the Leonian medium. A feltlike surface weft 1 to 1.5 mm. deep is formed by parallel, dichotomously branched, radially directed, coarse hyphae. A loose superficial weft 2 to 5 mm. deep is composed of granular-walled, coarse hyphae, which soon become brown. The surface layer produced in cultures is apparently homologous to the blue-black crust on collected material, and the superficial weft corresponds to the brown subiculum upon which the fructifications are usually seated. Of all the species cultured this showed greatest vegetative vigor (see Table I). The fungus was cultured on cork-decoction agar, on oak wood, and on granulated cork, with various nutrient concentrations. These media reduced vegetative growth in varying degrees, but none of the cultures produced the pycnidial stage observed in field material.

Observed associations. — The writer discovered a pycnidial stage (Pl. XXXIV, Fig. 5) associated with the perfect stage on a much-decayed oak log in low ground bordering a tamarack swamp. A blue-black area of several square feet was composed of numerous

imperfect fructifications. The pycnidia (Figs. 34 *A–B*) are of the Sphaeronaema type and differ from those described by the writer (30) for *G. parvulum* in that they are loosely aggregated and not cespitose, being more or less equally scattered, and in that they are more robust, with slightly larger sporulating cells. The latter measure 6–11 × 2.5 μ. The pycnidia measure (150) 170 to 200 (215) μ in width and (100) 120 to 140 (180) μ in height, exclusive of the beak. Beaks are 50 to 200 μ in length, averaging

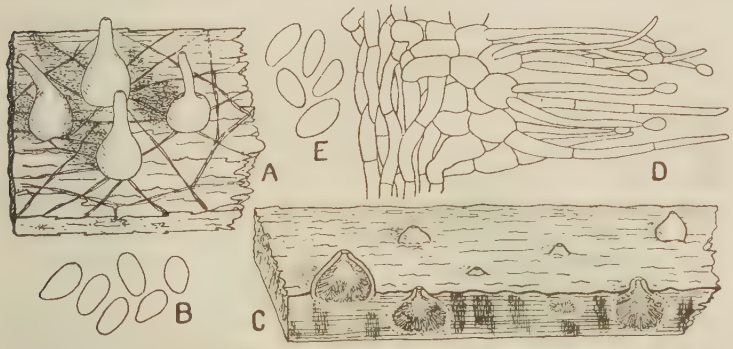

Fig. 34. *A–B, Glonium stellatum;* the *Sphaeronaema byssoideum* stage. *A*, pycnidia, × 30; *B*, pycnidiospores; all from field material. *C–E, Glonium lineare;* pycnidial stage from field material. *C*, habit of pycnidia, × 30; *D*, portion from lateral wall showing the cells of the wall and the sporulating cells; *E*, pycnidiospores

140, and have an average median diameter of 60 μ. The pycnidia are superficial upon the loose subiculum in the less-exposed areas, whereas on exposed surfaces they are superficial upon the thin black crust. The stage name **Sphaeronaema byssoideum** Lohman, status novus *Glonii stellati*, is suggested. For other details the description of *Sphaeronaema parvulum* (30, p. 152) is sufficient. All attempts to stimulate germination of the pycnidiospores were unsuccessful.

Glonium simulans Ger. (Pl. XXXIV, Fig. 4)

No. 30. On decorticated wood of *Tilia americana* L., Ann Arbor, Mich., Nov. 15, 1928. Collected by M. L. Lohman.

G. simulans is not uncommon about Ann Arbor on old wood of Quercus, Tilia, and Ulmus, and on old stumps of Juglans and Prunus. The spores are elliptic-biconical and measure 14–16 (18) × (4.5) 5–6 μ, somewhat larger than Ellis (12, p. 683) described them.

Vegetative cultural characteristics. — Growing mycelia of *G. simulans* are gray ("dawn gray," soon becoming "storm gray") and the superficial weft retains this color for several months. The feltlike surface layer is darker, especially on the Leonian medium, and is composed of irregularly branched, closely interwoven, brown, granular-walled hyphae and coarse, black strands of parallel, anastomosing filaments. On the Leonian medium these strands occasionally become aërial and branch dendroidally. The "purple-drab" coloration of the oatmeal medium extends as much as two centimeters beyond the margin of the culture. In its mode of spore germination (31) and in its cultural characteristics, the species is intermediate between *G. stellatum* and *G. parvulum.* It approaches the former in its rate of growth, texture of the three layers on agar media, granular-walled hyphae, and straight, radially directed parallel strands. In the color of the young mycelia and in the distinct coloration of the oatmeal medium it suggests *G. parvulum.* All the cultures remained sterile, and pycnidia were not observed in the field material.

Glonium parvulum (Ger.) Cooke

No. 12. On decorticated trunk of *Ulmus fulva* Michx., Ingham County, Mich., Oct. 14, 1928. Collected by M. L. Lohman.

The original material used for culture notes on this species has been described and figured by the writer (30).

Vegetative cultural characteristics. — *G. parvulum,* in its cultural characteristics, is distinct from the two preceding species. The young mycelium is at first whitish, but soon becomes pinkish and then "spinel red" to "hellebore red." At six to ten weeks cultures are erumpent, with an irregular margin, and a single culture may show various colorations, including "vinaceous," "pinkish cinnamon," "vinaceous-fawn," and "avellaneous." In the light the

oatmeal medium is greatly discolored ("purplish vinaceous" or "purple-drab").

Cultural fructifications. — A pycnidial stage has been obtained on numerous single-spore and single-ascus cultures under various conditions. Single germinating pycnidiospores were isolated and these returned the pycnidial stage. For a detailed description of pycnidial development and discussion on the taxonomic position of the pycnidial stage the reader is referred to an earlier report (30). The name *Sphaeronaema parvulum* was suggested, and the description of the pycnidial stage was presented as a supplement to that of the perfect stage. The description is referable to *Sphaeronaema parvulum* Lohman, status novus *Glonii parvuli* (*Hysterium* (*Glonium*) *parvulum*, Gerard, *Bull. Torr. Bot. Club*, 5 : 40. 1874).

The diagnosis was based upon development from single ascospores on various culture media and on oak chips on the surface of an oak-infusion medium. It was stated (*op. cit.*, p. 150) that pycnidia obtained from single-conidium (pycnidiospore) cultures were merely conic-ostiolate, but typical pycnidia have since been obtained on such cultures.

Sphaeronaema parvulum and *S. byssoideum* are near the Pleuronaema type of the Von Höhnel system (20). They differ from it in the thinner pycnidial wall, in the smaller and not definitely allantoid spores, and, primarily, in that the spores are not pleurogenetic as well as acrogenetic.

Observed associations. — After the author published the description of the pycnidial stage obtained in culture (30), a small collection of *G. parvulum* (Lohman, No. 240; Univ. of Mich. Herb.) was made on much-decayed oak, and it presented the pycnidial stage identical in all respects with that already described and figured by the writer.

Glonium lineare (Fr.) De Not.

No. 255. On weathered slab of *Fraxinus nigra* Marsh., Livingston County, Mich., July 27, 1930. Collected by M. L. Lohman.

Asci 55–65 × 12 14 μ; spores 2-celled, hyaline, 13–16 × 6–8 μ, oblong and the upper cell well rounded.

Vegetative cultural characteristics. — *G. lineare*, in its vegetative characteristics, differs decidedly from the three preceding species. The superficial and surface layers together are less than one millimeter deep. The sparse aërial mycelium is white, becoming gray on cultures that have developed for several months. The surface layer is at first light in color, but soon becomes a sordid green ("Andover" to "dark ivy green"), and this persists several months. Then numerous stromatic erumpent areas, becoming 0.5 to 1 mm. in diameter and later confluent, form progressively from the central region outward and blacken the culture. After three months the pycnidial cavities described below were abundant in the stromatic areas and in isolated darkened areas on the margins. Coarse vesicular hyphae are abundant in the surface layer and brown, terminal or intercalary vesicles 8 to 12 μ in diameter are numerous in old cultures. The species grows very slowly.

Cultural fructifications. — Three to eight independent cavities arise beneath each stromatic elevation, apparently by the dissolution of large vesicular hyphae. A wall about each cavity is first discernible as several layers of hyaline, long-celled filaments oriented in a direction perpendicular to the surface of the stroma. This tissue later becomes dark, averages 10 to 20 μ in thickness, and the inner filaments branch inwardly to form short, swollen cells, each of which bears a number of tufted sporulating cells and occasionally a sterile septate filament 40 to 60 μ in length. Individual sporulating cells are simple, curved at the base, measure 15–30 $\times$ 2–2.5 μ, and abstrict the hyaline pycnidiospores singly from their tips. The spores are elliptic-oblong to ovate-inequilateral, and measure 2.5–3 $\times$ 1.5–2 μ. The cavities increase until their walls meet, but apparently they do not coalesce. True, ostiolate pycnidia do not develop, and the conidial discharge to the surface of the stroma is irregular.

Observed associations. — The thin, black stroma on wood is accompanied by numerous pycnidia (Fig. 34 *C–E*) and this condition precedes and borders the hysterothecial stage. The globular, black, carbonaceous, conic-ostiolate pycnidia arise within the wood and beneath the stroma and at maturity become erum-

pent by their short papillae. It is possible, however, to find pycnidia entirely superficial upon the stroma. In the latter condition pycnidial walls are complete, small-celled prosenchymatous, and 15 to 30 μ thick, whereas in the former types blackening occurs only in the exposed papillate portions, and the lower lateral and basal walls are hyaline and poorly developed. The spore-bearing cells and spores conform to the type obtained in culture. Pycnidia measure (150) 200 to 300 μ in diameter.

This type of fructification falls in the Plenodomus-Dothiopsis-Phomopsis group of Diedicke's system (8). These form genera are distinguished with difficulty, and intermediate forms are to be expected. *G. lineare* pycnidia approach Phomopsis in the type of spore-bearing cell and in the spatial relations of the wall to the substratum, but in their spores and in the sclerotic development of the wall they are of the Plenodomus type, if the diagnostic characters of Diedicke are used (7).

The pycnidial stage of this species (see p. 232) has recently been described as *Hysteropycnis globularis* Hilitzer (18, p. 151).

Mytilidion tortile (Schw.) Sacc. (Pl. XXXIV, Fig. 1)

No. 262. On bark of living *Juniperus virginiana* L., Washtenaw County, Mich., Aug. 13, 1930. Collected by M. L. Lohman.

Hysterothecia loosely gregarious and inordinately arranged, superficial, black, occasionally longitudinally striate, (0.5) 0.7 to 1.2 (1.5) mm. in length, 0.2 to 0.3 mm. in breadth, the height equaling or slightly exceeding the width, subconchiform and rounded above or elongate with pointed ends and then usually acutely keeled; walls prosenchymatous, thin, carbonaceous, and fragile; asci slender-clavate, (65) 75–85 $\times$ 6–8 μ, the inner ascus becoming 115 to 130 μ in length on expansion; paraphyses abundant, 2 μ in diameter, hyaline, septate, irregularly branched above, forming a yellowish epithecium; spores obliquely uniseriate, clear yellow-brown to slate-brown, 3-septate, 13–16 (18) $\times$ 4–5 μ or very rarely 20 μ long and 4-septate, mostly oblong-fusiform and slightly curved, with obtuse ends and slight constrictions.

This description is given since serious discrepancies occur

among those that have been published under the name of *M. tortile* (Schw.) Sacc. It is based upon collected material, upon Ellis and Everhart 2152 and 2829, North Am. Fungi, and upon 2065 in the herbarium of Schweinitz at Philadelphia.

Ellis (12, p. 688) correctly disposed of his *M. Juniperi* E. & E. (*Journ. Myc.*, 4 : 57. 1888) by placing the name in synonymy. Rehm (38, p. 110) altered his earlier description (36, p. 23), making it conform to the Ellis and Everhart distributions, and at the same time he placed *M. decipiens* (Karst.) Sacc. in synonymy. The disposition of the latter must be accepted provisionally in view of the writer's notes presented under that name.

It must not be forgotten that Schweinitz (43, p. 50) described his *H. tortile* on Carolina material (No. 250, on bark of *Juniperus virginiana*) and that no one has stated definitely that Schweinitz 250 and 2065 are identical microscopically. Duby (9, p. 38) described the spores of Schweinitz 250 as being light brown, 3-septate, and three to four times as long as broad, whereas Rehm's (35, p. 187) revision notes refer only to "*H. tortile* Fr. ex herb. Hooker," which Rehm labeled "Unbrauchbares Exemplar."

Vegetative cultural characteristics. — In cultures the young marginal hyphae are dark ("mummy brown" to "fuscous black"); a loose, thin, superficial layer lighter in color ("cinnamon-brown") develops tardily; and an unusual discoloration ("vinaceous-fawn" to "cinnamon-drab") of the oatmeal appears early and persists. Single-spore and single-ascus cultures produced a pycnidial stage on the Leonian medium and on cork-decoction agar.

Cultural fructifications. — Pycnidia (Figs. 35 *A–B*) are single or clustered in the aërial mycelium and densely clustered in stromatic areas of the surface layer. They are globular, conic-ostiolate, 90 to 150 (175) μ in diameter, and have a complete, thin, fragile, and decidedly carbonaceous wall. The wall is 10 to 20 μ in thickness, with the outer third portion opaque-carbonaceous, and the inner layers hyaline-prosenchymatous. Young pycnidia show a central portion of interwoven vesicular hyphae, and spore production apparently begins without a definite cavity being formed. Later, the pycnidia contain an agglutinated mass of

spores and disintegrated hyphae held in a mucilaginous oily matrix, which imbibes water very slowly. In old pycnidia the spore-bearing cells are obovate and measure 4–6 × 3 μ. They are arranged in an irregular layer upon an indefinite hymenial base (Fig. 35 *F*). The pycnidiospores are acrogenetic, hyaline, subglobose, 2 μ in diameter, and appear to be abstricted singly. Hilitzer (18, p. 135)

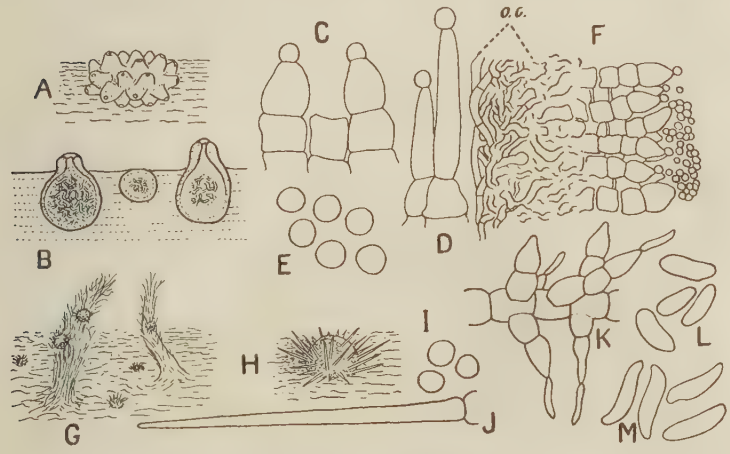

Fig. 35. *A–F, Mytilidion tortile;* pycnidial stage obtained in culture. *A*, pycnidial cluster on agar medium, × 25; *B*, sectional view of pycnidia in the surface layer; *C*, *D*, spore-bearing cells (*D*, uncommon); *E*, pycnidiospores; *F*, portion from lateral wall showing cells of the wall and spore-bearing cells (*o.c.*, region of opaque cells). *G–M, Mytilidion decipiens;* pycnidial and hyphomycetous (*K–M*) stages obtained in culture. *G*, erect mycelial tufts and pycnidial fructifications on agar medium, × 30; *H*, pycnidium, × 100; *I*, pycnidiospores; *J*, a spine from the surface; *K*, conidiophores of the hyphomycetous stage; *L*, conidia from the surface layer; *M*, conidia from the hyphae of the superficial layer and the erect tufts

has described a similar pycnidial stage in connection with *M. aggregatum* Duby.

Observed associations. — Fragile, carbonaceous, globular pycnidia 75 to 100 μ in diameter are abundant on collected material and on "Schweinitz 2065." They are single, ostiolate, and

erumpently superficial. Numerous examinations did not reveal a hymenial content that could be satisfactorily interpreted, although an agglutinated mass of indefinite structure was occasionally observed.

Mytilidion laeviusculum (Karst.) Sacc.

No. 281. On unexposed surfaces, much-decayed log of *Larix laricina* (Du Roi) Koch, Livingston County, Mich., Sept. 18, 1930. Collected by M. L. Lohman.

Hysterothecia 0.4–0.5 × 0.25 mm.; asci 50–65 × 6–7 μ; spores 18–22 × 2.5 (3) μ, spindle-shaped and 3- or 4-septate.[3]

Vegetative cultural characteristics. — Cultures of this fungus differ from those of *M. tortile* in that growth is far more rapid, the marginal mycelium is darker ("sooty black"), the superficial layer is a deeper brown "Prout's brown" to "bister"), and there is no discoloration of the oatmeal medium. Cultures resemble closely those of *G. stellatum*, but radial growth is by repeated irregular branching of uniform, interwoven hyphae, and not by the straight paralleling hyphae of that species. Terminal and intercalary brown vesicles are abundant in the surface layer. Imperfect stages are unknown.

Mytilidion decipiens (Karst.) Sacc.

No. 302. On inner bark, old stumps of *Picea canadensis* (Mill) BSP., Dickinson County, Mich. (N.P.), Sept. 3, 1930. Collected by A. H. Smith.

Hysterothecia 0.3–0.5 (0.6) × 0.1 0.2 mm., about as high as broad, with the swollen central portion faintly striated and the acuminate, smooth ends free from the substratum; asci 75–90 × 8–10 μ; paraphyses hyaline, much-branched, and interwoven above; spores 15–21 × 5–6 μ, clear yellow-brown, subbiseriate, 3-septate, unconstricted, slightly curved, oblong-elliptic with

[3] These measurements are practically identical with those given by Karsten (22, p. 261) in his original description of *Lophium laeviusculum*. Individual fruits of *M. tortile* are noticeable to the naked eye, whereas the aggregated hysterothecia in the material herein referred to *M. laeviusculum* are seen only as a purple-black coloration of the substratum.

obtuse ends, the lower cell in most specimens narrower than the upper.[4]

Rehm (38, p. 110), listing Karsten's Fung. Fenn. 767, placed *M. decipiens* (Karst.) Sacc. in the synonymy of *M. tortile*. Since that number has not been studied by the writer the material at hand can be only questionably referred to *M. decipiens*. However, in its cultural characteristics and in its morphology, the writer's material indicates an organism distinct from *M. tortile*. In view of the state of confusion now existing in the taxonomy of the group, it is best to refer the data tentatively to Karsten's species until the validity of Rehm's disposition of that species is further investigated.

Single-ascus isolations were not obtained for this species. All single-spore cultures originated with the isolation of germinating spores from several plates prepared from the same spore suspension. The unexpected character of the resulting cultures demands that this species be restudied with additional isolations. Since all cultures were identical and apparently the expressions of a single organism, the results are given herein, pending a further investigation of the cultural habits of this collection.

Vegetative cultural characteristics. — Young mycelia are white, with a very thin superficial growth; the radial growth is confined to the medium. The hyphae are short-septate, 3 μ in diameter, with variously swollen cells, and anastomose in thick strands; they branch profusely and irregularly, and show a dense-oily content. The mycelium soon becomes pale orange-yellow ("ochraceous-buff"), and the Leonian and oatmeal media are readily discolored "honey-yellow." When mass conidial production begins on the surface the culture becomes darker ("orange-cinnamon"). On the Leonian medium at three months the surface layer becomes dark brown. Old cultures also show thick, erect tufts of anastomosed hyphae, which bear numerous conidia.

Cultural fructifications. — The aërial hyphae bear clusters of

[4] The description indicates that the spores are intermediate in character between those of *M. tortile* and *M. laeviusculum*. Karsten's original description (22, p. 261) of *Lophium decipiens* (Fung. Fenn. 767) suggests a fructification with the characteristics related above, except that the hysterothecia are described by Karsten as being somewhat smaller.

long-elliptic to curved or sigmoid conidia (Fig. 35 *M*) on intercalary swollen cells. These conidia are subhyaline under the microscope, orange in mass, and measure 5 8 × 1.5–2 μ. Within the surface layer hyphal cells branch laterally to form tapering conidiophores 6 to 10 μ in length, which abstrict conidia from their tips. These conidia (Fig. 35 *L*) are elliptic to inequilateral and measure 4–6 × 1.5–2 μ.

Pycnidia (Figs. 35 *G–H*) arise singly in the erect hyphal tufts, and on the margin in old cultures they develop within the surface layer. The walls are small-celled parenchymatous, membranous-carbonaceous, and the outer cells develop unseptate, brown, pointed bristles 40 to 60 μ in length. Young pycnidia show an agglutinated hyaline, central portion of indefinite structure, apparently densely packed with oil. Subglobose to short-oblong hyaline pycnidiospores 1.5 μ in diameter or 2 × 1.5 μ are produced and retained within an oily matrix. Definite sporulating cells have not been observed. The fructification is of the Pyrenochaeta type in the sense of Diedicke (8). The indefinite manner of pycnidiospore production would refer it to the Sclerochaeta type of the Von Höhnel (20) system.

The imperfect stages have not been observed in collected material.

Mytilidion resinicola Lohman, sp. nov. (Fig. 36)

Hysterotheciis subgregariis et inordinate dispositis, superficialibus, rectis, nigris, rugosi-punctatis vel indistincte longitudinaliter striatis, 0.75–1.25 mm. longis, 0.25–0.3 mm. latis, subconchiformibus cum labiis acutissimis vel depressi-hysteriformibus, interdum triradiatim ramosis, plerumque ad crustam nigram carbonaceam hypharum dense intertextarum conjunctis, textura prosenchymatosis, fragilibus carbonaceis; ascis clavatis, octosporis, 100–110 × 15 μ; membrana ascorum crassa; paraphysibus filiformibus, septatis, multiramosis et sursum intertextis; sporidiis 24–26 × 8 9 μ, distichis vel oblique monostichis, oblongo-ellipsoideis, luteofuscis vel fuligineis et fere opacis, 3-septatis, ad septa valide constrictis.

Ad corticem resinosum in truncis mortuis *Laricis laricinae*, solum ad basim ramorum vetustorum. Livingston County, Mich., Aug. 6, 1930. Specimen typicum in Herb. Univ. Mich.

Hysterothecia loosely gregarious and lying in various directions, superficial, straight, black, rugose-punctate to faintly longitudinally striate, 0.75–1.25 × 0.25–0.3 mm., subconchiform with a sharp ridge or depressed hysteriform, occasionally 3-radiate, accompanied by a compact, black carbonaceous crust of close-septate, torulose, interwoven hyphae; walls prosenchymatous, thin, carbonaceous, and fragile; asci double-walled, 100–110 × 15 μ; paraphyses hyaline, septate, much branched, and interwoven above; spores 24–26 × 8–9 μ, elliptic-oblong with rounded ends, 3-septate and deeply constricted at the septa, yellow-brown to dark fuscous and nearly opaque, and biseriate, becoming obliquely uniseriate in the extended inner ascus.

On resinous exudation and the surrounding bark, confined to knots on fallen and erect dead trunks of *Larix laricina* (Du Roi) Koch, Livingston County, Mich., Aug. 6, 1930. Collected by M. L. Lohman (No. 260). Type in the herbarium of the University of Michigan.

The asci and spores are similar to those of *Hysterium angustatum* Alb. & Schw., but the hysterothecia have the form and texture of Mytilidion. In its diagnostic features the fungus approaches *M. aggregatum* (DC.) Duby (9, p. 34) and *M. rhenanum* Fuckel, as used by Rehm (36, p. 24). It differs from the former in that the spores are larger with all of the cells colored, and from the latter in that the spores are broader and constricted. According to Rehm (*op. cit.* and 35, p. 181) the status of these two species has not been determined with any satisfaction.

Vegetative cultural characteristics. — In respect to the vegetative character, cultures of this species closely resemble those of *M. tortile*. The young mycelia, however, are gray rather than brown, the pink discoloration of the oatmeal does not persist, and growth is more rapid. Only single-ascus isolations were obtained, and these have remained sterile.

Observed associations. — The pycnidia (Fig. 36 *E*) accompanying the hysterothecia are ostiolate-papillate, 200 to 250 μ in diameter, smooth and globose with a prosenchymatous, fragile-carbonaceous, complete wall 5 to 8 μ thick. The simple sporulating cells measure 5–10 × 2.5 μ and abstrict singly from their tips;

hyaline, subglobose pycnidiospores, 2 to 2.5 μ in diameter. The spores are held in a mucilaginous matrix and on drying form a white concretion at the tip of the papilla. This type of fructification can be referred to the form genus Aposphaeria.

Mytilidion Thujarum (C. & P.) Lohman, comb. nov. (*Hysterium Thujarum*, Cooke, *Disc. of U. S.*, p. 33. 1875).
(Pl. XXXIV, Fig. 2).

No. 306. On inner bark, old stumps of *Thuja occidentalis* L., Brown County, Wis., Sept. 8, 1930. Collected by A. H. Smith. Hysterothecia 0.4–0.8 (1) $\times$ 0.25–0.4 mm.; asci 140–170 $\times$

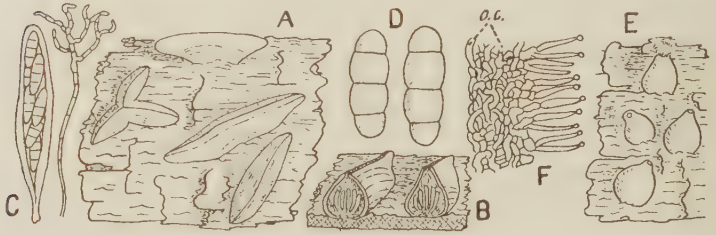

FIG. 36. *Mytilidion resinicola;* from field material. *A*, hysterothecia, $\times$ 20; *B*, cross-section view; *C–D*, hymenial elements; *E*, pycnidia, $\times$ 20; *F*, portion from lateral wall showing cells of the wall, the slender-clavate spore-bearing cells and the minute, subglobose pycnidiospores (*o.c.*, region of opaque cells)

15–18 μ; spores 34–40 $\times$ 10–12 μ, rich brown, slightly curved, pointed below, 4- to 5 (6)-septate, constricted at the septa, with the third cell from the upper end swollen. The type (?), "*H. thuiarum* C." at Kew, has been examined by the writer. That material is described by Bisby (as cited in note 1).

Young hysterothecia are black and shining, vertically compressed, with pointed ends and a sharp ridge, and as they develop the crest becomes obtusely rounded and more or less distinctly longitudinally striate. Of greater importance in the proper classification of this species is the fact that even at maturity the walls of the hysterothecium are thin and fragile, with the structure of Mytilidion.

Vegetative cultural characteristics. — The species is distinguished from *M. tortile* in culture by the more dense, and deeper brown, superficial layer and by the close, dendroidal branching of the hyphae in this and the surface layer. Cultures on various media, held under the same conditions as those of *M. tortile*, did not produce pycnidia. Empty pycnidial fruits comparable to those observed in *M. tortile* are abundant in the collected material which shows hysterothecia in all stages of development.

Hysterium pulicare Pers. ex Fr.

No. 198. On bark of *Ulmus americana* L., Ann Arbor, Mich., April 4, 1930. Collected by M. L. Lohman.

Adequate descriptions of the species have been given by Rehm (36) and by Ellis (12). The writer's studies, however, indicate that the coloration of the end cells of the spores is variable within a given hysterothecium. Typical germination of *H. pulicare* spores is by one or two germ hyphae from each of the terminal cells. Many spores were studied and germination of the brown central cells was estimated as less than 5 per cent. Germination in these cells and in the occasional, brown terminal cells was considerably delayed, whereas in the brown terminal cells of *H. angustatum* spores it proceeded readily. The germ tubes of *H. pulicare* ascospores are densely oily-granular.

Vegetative cultural characteristics. — Cultures are black and present a smooth, shining surface due to the absence of the superficial layer. A loose, thin, gray superficial layer of very delicate hyphae does appear on the oatmeal medium after five or six months. The origin of these hyphae is twofold: (1) the germination of pycnidiospores to produce the more dense mycelial clusters; (2) the germination of thick-walled resting cells of the surface layer to produce an even, widespread, loose, mycelial weft. Various cells of the hyphae of the surface layer become pyriform or globular and store a tremendous amount of oil. They may be single and terminal on short branches, or intercalary and occurring either singly or in chains. Olive-brown, thick-walled cells of this type attain a diameter of 8 to 12 μ.

Cultural fructifications. — Pycnidiospores were not observed

in cultures on the Leonian medium at 20 to 25° C., although pycnidial cavities were produced sparingly on this medium at 10° C. On the oatmeal medium at the higher temperatures sporulating pycnidial cavities were fairly common by the fifth or sixth month, and at that time in the cultures at 10° C. pycnidiospores were being produced in abundance in well-developed pycnidia. The illustrations (Figs. 37 *B–C*) and description of this stage pertain to the pycnidia obtained in the latter cultures.

Pycnidia 75–150 μ in diameter arise within the surface layer and become ostiolate-erumpent. They are single or clustered,

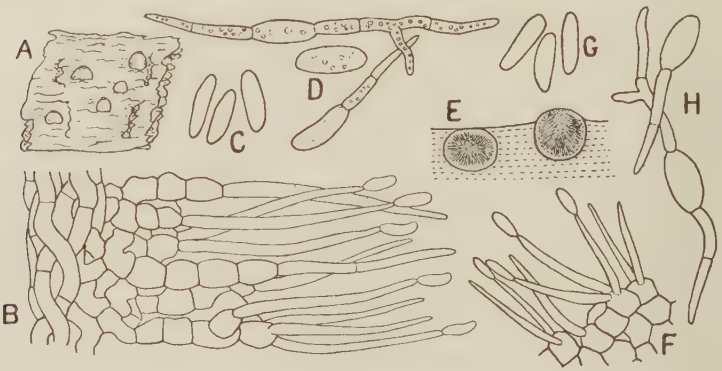

Fig. 37. *A–D, Hysterium pulicare;* pycnidial stage. *A*, pycnidia on Quercus bark, × 30; *B*, portion from lateral wall showing cells of the wall, spore-bearing cells and pycnidiospores (typical for field material and for pycnidia obtained in culture); *C*, pycnidiospores from cultures; *D*, germinating pycnidiospores from field material. *E–H, Hysterium insidens;* pycnidial stage. *E*, pycnidial cavities in the surface layer on agar medium, × 70; *F*, pycnidiospores and spore-bearing cells; *G*, pycnidiospores; *H*, early germination of the same; all from cultures

and each has a single cavity. Their walls are membranous, with the outer layers loose-prosenchymatous. Hyphae of this tissue branch inwardly as tapering filaments with globular basal cells, and each filament is terminated by a slender sporulating cell. The filaments extend through an indefinitely small-celled, parenchymatous, hyaline layer, which gives rise to numerous slender sporulating cells measuring (15) 25–50 × 1.5–2 μ. The

hyaline, cylindric-inequilateral pycnidiospores are acrogenetic and measure 4–5.5 × 1.5 (2) μ. Pycnidiospores in various stages of germination have been observed. The germ-tube hyphae have a densely granular protoplasmic content as noted for the germinating ascospores.

Observed associations. — The original material for these cultures does not show a pycnidial stage. Another collection on Quercus bark is accompanied by numerous black, membranous, globular, superficial, ostiolate pycnidia (Fig. 37 *A*), 50 to 75 μ in diameter, with pycnidiospores and spore-bearing filaments of the type described above. Pycnidiospores from this material were germinated (Fig. 37 *D*). This confirms Brefeld's (2, p. 47) statement concerning Möller's studies on this species. The pycnidial stage (see p. 232) recently described for this species by Hilitzer (18) as *Hysteropycnis occulta* is similar.

Hysterium angustatum Alb. & Schw.

No. 309. On bark and wood, living *Betula alba* var. *papyrifera* (Marsh.) Spach., Brown County, Wis., Sept. 8, 1930. Collected by A. H. Smith. This material is tentatively referred to *H. angustatum.*

Hysterothecia (0.6) 0.8–1.2 × 0.4 mm., oblong, rounded above with a prominent fissure, rugose-punctate to faintly longitudinally striate, straight to subflexuous, densely aggregated, mostly irregularly oriented, and superficial upon a greenish black crust dense with algal cells; asci 105–120 × 10–16 μ, including the stalk; paraphyses filiform, much branched above and forming an epithecium; spores 22–26 × 6.5 8 (9) μ, biseriate, elliptic-fusiform, and slightly curved, rich brown and 3-septate with the cells swollen.

Ellis (12) and Rehm (36, 38) have indicated the difficulty with which *H. pulicare* and *angustatum* are separable, and Rehm has questioned the specific value of the latter. The writer's material combines beautifully the diagnostic features of the two species. Yet in its cultural character the fungus does not suggest *H. pulicare* in any respect.

Vegetative cultural characteristics. — Growing mycelia are white

and cultures remain light for several weeks. The surface layer then darkens ("Andover green"), and this color is pronounced until hidden in old cultures by a deep superficial layer of coarse, straight, sparingly branched hyphae, "dark olive-gray" in mass. Erect, green, dendroid tufts of anastomosed filaments from the surface layer occasionally break through the superficial weft. The oatmeal medium is discolored to "light brownish vinaceous." In mycelial color changes, rate of growth, and discoloration of the medium the cultures resemble those of *H. insidens*.

Hysterium insidens Schw. (Pl. XXXV, Fig. 3)

No. 102. On Quercus palings, Preble County, Ohio, Sept. 11, 1929. No. 257 (Septonema stage): on old rail (Quercus ?), Livingston County, Mich., July 26, 1930. No. 308 (hysterothecial and Septonema stages): on Quercus palings, Ann Arbor, Mich., Oct. 17, 1930. All collections by M. L. Lohman.[5]

The hysterothecial stage has been collected only on Quercus, by the writer, and the common habitat is exposed medullary rays on radial surfaces of rails and palings. Rail and picket fences, now seldom seen, invariably yield this species. The conidial stage is not uncommon on decorticated limbs of Quercus, but the hysterothecial stage has been found only once in such habitat.

Vegetative cultural characteristics. — Vigorously growing mycelium is white and many cultures remain light in color for several weeks. Ordinarily by the third week the superficial layer darkens ("vetiver green") and the narrow margin, the bare surface layer, is "yellowish olive." In older cultures the nonsporiferous mycelium remains light brown ("avellaneous" to "wood" or "clove brown"). When the hyphomycetous stage

[5] In the writer's material from Ohio and Michigan the general appearance is that of the form called *H. complantatum* Duby (9, p. 38; cf. Ellis and Everhart 460, North Am. Fungi), but the average spore is larger and has more septa. Hysterothecia as large and as prominent as those in Ellis and Everhart 3129, North Am. Fungi, are rare. The asci measure 90–110 (125) × (15) 18–20 μ and the spores (25) 28–35 (40) × 8–10 μ. Spores 28 to 35 μ in length are 6–8-septate, and the larger spores are 8–10-septate. It is either the third or fourth cell from the upper end which is swollen, depending upon the number of septa. Ellis (12, p. 696) questionably referred the European *H. Berengerii* Sacc., of similar habitat, to this species.

is abundant, cultures are much darker. The coloration of the oatmeal medium is variable, and this condition appears to be linked with variations in the vegetative expression of different single-spore cultures from the same hysterothecium. The oatmeal medium may be only slightly darkened or it may become a persistent red-brown ("burnt lake" or "madder brown"). The former condition is general for ascus and ascospore cultures which produce pycnidia and for pycnidiospore cultures, whereas the deep coloration accompanies abundant conidial production and is pronounced in single-conidium cultures regardless of the amount of sporulation. Elliott (10) reported a red-brown chromogenesis of the culture medium for certain species of Alternaria, and noted that the strain of *A. solani* from potato produced a discoloration, but the strain from Datura did not. Elliott, however, correlated deep chromogenesis with non-sporulating cultures and the lack of coloration with abundant conidial production.

Cultural fructifications. — The Septonema stage first appears as brown erect tufts near the margin. These tufts are composed of sparingly branched tortulose hyphae, arising as vertical branches from similar hyphae in the surface layer. Swollen cells later become septate, deeply constricted at the new and old septa, and finally each of the two cells of a potential conidium becomes cross-septate. Mature conidia (Fig. 38 *F*) of the normal type are 4-celled, deep fuscous, granular-walled, much constricted at the central septum, and measure 15–18 × 5–6.5 μ. They do not separate readily, and chains of six to ten or twelve are not uncommon. Chains of 1- and 2-celled conidia, of muriform conidia, and of sclerotic bodies are also developed (Figs. 38 *I–L*). All types of sporulation germinate readily in distilled water and many of them *in situ* under the moist conditions of bulk-medium cultures. In old cultures, particularly on the Leonian medium, there are clusters of interwoven conidial chains within the surface layer. A single-ascus culture is illustrated (Fig. 31) in which the entire surface is darkened by Septonema conidia.

To determine Septonema conidial development in culture, this imperfect stage was isolated from field material of two sources, one collection being in association with *H. insidens* hysterothecia

and the other free and from another locality. Conidial development in these single-conidium cultures was identical with the sporulation in ascospore and ascus cultures. Single pycnidiospores obtained from a single-ascospore culture were germinated, and six single-spore isolations were made. These cultures ran four months

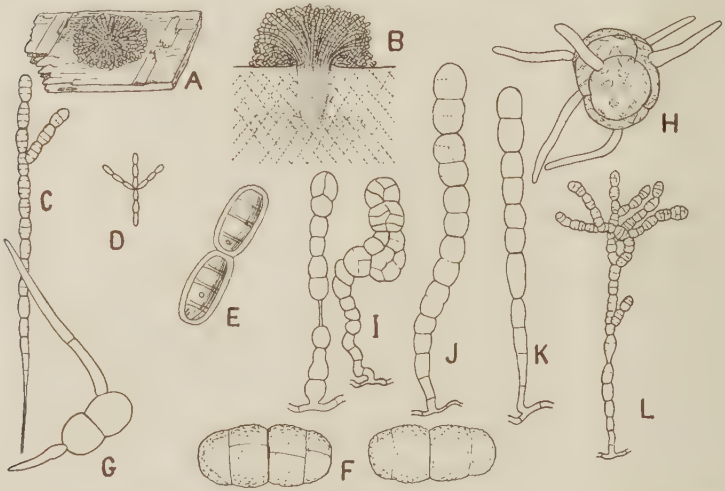

FIG. 38. *Hysterium insidens;* the *Septonema spilomeum* stage. *A*, conidial fructification on much-weathered Quercus rail, × 10; *B*, vertical section showing point of origin of conidial filaments; *C*, a typical filament; *D–E*, the illustrations by Berkeley, after Cooke (*Handbook Brit. Fungi*, 1 : 481. 1871); *F*, typical mature spores from cultures and field material; *G*, germination of a young conidium obtained in culture; *H*, germination of a mature conidium from field material; *I–L*, conidial filaments obtained in cultures

and did not return typical Septonema conidia, although the characteristic surface layer of torulose hyphae was developed. The original strain, however, has produced the Septonema stage very sparingly.

Pycnidiospores are produced (Figs. 37 *E–H*) in cavities 90 to 150 μ in diameter. These are largely confined to the surface layer, and the pycnidiospores are discovered only upon microscopic examination of this layer. The surrounding wall is complete,

brown, small-celled parenchymatous, and averages 10 to 15 μ in diameter. The sporulating cells are simple, clustered, and measure 5–8 × 1–1.5 μ. The pycnidiospores are hyaline, elongate-elliptic, inequilateral to suballantoid, acrogenetic, and measure (2.5) 3–4 × 1–1.5 μ.

Observed associations. — The Septonema stage (Figs. 38 *A–C*), which usually accompanies in a weathered condition the hysterothecial stage, was identified as *Septonema spilomeum* Berk. (*London Journ. Bot.*, 4:310; t. 12, Fig. 5. 1845), and a study of the type material (No. 92 from Ohio) in the herbarium of Berkeley proved the determination to be correct. In listing this imperfect stage Cooke (4, p. 481) reproduced Berkeley's figures, which are illustrated here (Figs. 38 *D–E*) for comparison, and correctly quoted Berkeley as follows:

> Forming little scattered sori about the size of a poppy seed; threads branched, articulations oblongo-elliptic, triseptate, one or more of the septa occasionally containing an oil globule, border of articulations pellucid, rough with little scabrous prominences. Very distinct in the punctiform habit, and in the nature of the articulations.

The description is true, but in need of revision. Berkeley's figures, which have been reproduced in taxonomic treatments of the hyphomycetous Fungi Imperfecti, do not accurately depict the characters of the material for which they have stood. The distinctive corrections are: (1) the conidia become larger progressively from base to apex of the conidial filament; (2) branching is seldom opposite; (3) conidia are much constricted at the central septum; and (4) a muriform condition is not uncommon in terminal conidia.

Fructifications bearing typical conidia are 0.5 to 2 mm. in diameter, at first greenish yellow, then red-brown and finally black, erumpent and globular by their massed conidial chains, but arising as a palisade of slender hyphae 0.5 to 1 mm. beneath the surface (Figs. 38 *A–B*). The fructifications are really deep-seated sporodochia. Typical conidia measure 15–21 (24) × (5) 6–7 μ, whereas the larger terminal conidia in old fructifications measure 25–28 (30) × 6–8 μ. Typical 3-septate conidia in the type specimen are smaller, measuring 15–18 × 7–8 μ, but conidial

measurements from other Ohio material in the herbarium of Berkeley agree. In several collections chains of typical conidia, with interconidial strands 4 to 10 μ in length, occur intermingled with normal Septonema chains. The isthmian chains are the basis for the form genus Polydesmus. Chains of muriform conidia are also met, and these represent Sirodesmium.

The type material of *S. spilomeum* presented two hysterothecia of *H. insidens*, and the Ellis distribution of it (North Am. Fungi 353) in the herbarium of the University of Michigan shows the perfect stage in fine condition. The Ellis distribution of *S. spilomeum* is identical with that of the type material. The *H. complanatum* Duby distributed by Ellis (North Am. Fungi 460) shows numerous *S. spilomeum* fructifications.

The pycnidial stage has been observed in collected material. The pycnidia are membranous-fragile, ostiolate-globular, 50 to 65 μ in diameter and 30 to 40 μ high, with brown, parenchymatous walls 6 to 10 μ in thickness. The hymenial elements agree with those obtained in culture, except that the pycnidiospores are somewhat longer, measuring 4–5 (6) $\times$ 1–1.5 μ.

Hysterographium kansense E. & E. (Pl. XXXV, Fig. 2)

No. 264. On bark of living *Quercus alba* L., Washtenaw County, Mich., Aug. 13, 1930. Collected by A. H. Smith and M. L. Lohman.[6]

This organism was fruiting so abundantly that an area of some fifteen square feet of bark was noticeably darkened.

Vegetative cultural characteristics. — Single-ascus isolations were not obtained for this species. The growing mycelium of single-spore cultures forms a velvety, erumpent mat, greenish slate ("deep slate green" to "iron gray") in color. In their color and composite growth the cultures resemble very much those of

[6] The material here referred to *H. kansense* E. & E. is identical with Ellis and Everhart 3037, North Am. Fungi, even in that the spores are considerably longer than Ellis (13, p. 22) described them. In the exsiccati the asci measure 130–140 $\times$ 15–18 μ and the spores (25) 30–36 $\times$ 8–10 μ. In the writer's material asci are 130–150 $\times$ 15–20 μ and the spores (29) 34–41 $\times$ 8–10 μ. Seaver (45) says that he examined the type material, and he notes no discrepancies in the measurements made by Ellis and gives identical measurements for his Iowa collections.

Hysterographium vulvatum. The surface layer is loosely stromatic; anastomosing is in the form of a conjunctive union of hyphal tips, and no pseudosclerotial development occurs. Cultures that have run four months have remained sterile.

Observed associations. — Only empty pycnidia accompany the perfect stage. They are superficial, single or aggregated, ostiolate-globular, with thin membranous walls, and measure 100 to 125 μ in diameter.

Hysterographium minutum Lohman, sp. nov. (Fig. 39)

Hysterotheciis 0.5–0.9 (1) mm. longis, 0.15–0.2 (0.25) mm. latis, nigris, supra complanatis cum labiis fere approximatis,

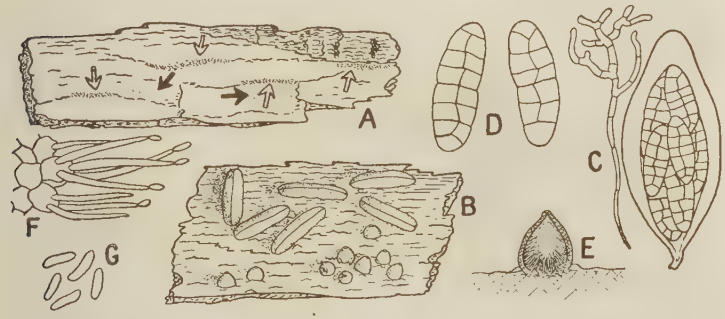

Fig. 39. *Hysterographium minutum;* hysterothecial and pycnidial stages from field material. *A*, portion of bark, natural size, arrows in outline indicate aggregations of hysterothecia and solid arrows indicate clusters of pycnidia; *B*, a small portion of same, × 20; *C–D*, hymenial elements; *E–G*, characters of the pycnidial stage

prominenter rugosi-punctatis, interdum longitudinaliter striatis, superficialiter erumpentibus, inordinatim in greges separatos, densos, elongatos, 6–10 mm. longos et 2 mm. crassos constipatis, ad rimas corticis exfoliati parallelas, textura carbonaceis, parenchymatosis cum loculis minutis; ascis octosporis, 65–75 × 20–26 μ, ellipsoideo-globosis aut subpyriformibus, abrupte brevistipitatis; paraphysibus septatis, sursum ramosis et epithecium crassum formantibus; sporidiis (20) 22–27 × 8–10 μ, inordinate tristichis, oblongo-ellipsoideis, luteolis vel fuscis, 5- vel 7-septatis et muriformibus, septo medio constrictis.

Copiose in cortice trunci vivi *Aceris saccharini*. *H. pachyasco* affinis, sed hysterotheciis non patelliformibus. Ann Arbor, Mich., Oct. 15, 1929. Specimen typicum in herb. Univ. Mich.

Hysterothecia 0.5–0.9 (1) × 0.15–0.2 (0.25) mm., flattened above with a narrow fissure, black and shining, prominently rugose-punctate, occasionally with several longitudinal striae above, erumpently superficial and variously oriented in isolated, dense, elongate aggregations 2 mm. in width and seldom exceeding 10 mm. in length, bordering the scars of exfoliation; walls small-celled parenchymatous, thick and carbonaceous; asci 65–75 × 20 26 μ, 8-spored, subpyriform or elliptic-globose, abruptly short-stipitate, double-walled with the inner wall thick-gelatinous; paraphyses branched and blackened above to form a thick epithecium; spores oblong-elliptic, (20) 22–27 × 8 10 μ, inordinately triseriate, clear yellowish to reddish brown, constricted at the central septum, becoming 5- to 7-septate, with a longitudinal division through all but the terminal cells.

Abundant on outer bark of trunk, *Acer saccharinum* L., Ann Arbor, Mich., Oct. 15, 1929. Collected by M. L. Lohman (No. 169). Type in the herbarium of the University of Michigan.

The most distinctive characters are the minute hysterothecia and the subpyriform to thick clavate asci of the Arthonia type. The asci of two described species of Hysterographium, namely, *H. pachyascum* Berl. and *H. hiascens* Rehm, approach this type. The latter species, however, although of similar habitat, has larger hysterothecia, much longer asci, and larger spores. Rehm referred material from Ellis to *H. hiascens*, and Ellis (12, p. 707) accepted the species for the coastal states. The writer's material approaches more closely the European *H. pachyascum*, which also has very small hysterothecia, similar spores, and asci which measure 60–70 × 15–20 μ. It differs from *H. pachyascum* in its habitat and in that the hysterothecia are not at all patelliform.

Vegetative cultural characteristics. — In its cultural features the fungus shows little resemblance to *H. kansense* or to *H. Mori*. It is of rapid growth and vigorous mycelia are scarcely distinguishable from those of *G. simulans*. The dendroid tufts are larger than those in cultures of *G. simulans*, and there is no discoloration

of the medium. The central fascicle of the erect tufts is in many cases 30 to 40 μ in diameter, and is composed of numerous, parallel, anastomosed hyphae. Sporulation has not been observed in culture.

Observed associations. — The ostiolate, obovate pycnidia are superficial, single or aggregated, seated in the outer cell layers of the bark, and measure 125 to 200 μ in diameter. The wall is thin, black, and subcarbonaceous laterally, poorly developed and unblackened below, i.e. of the Aposphaeria (?) type; tufted, slender, sporulating cells, measuring 5–8 $\times$ 1 μ, line the basal and lateral walls. The pycnidiospores are acrogenetic, hyaline, cylindric-inequilateral, and measure 2–2.5 $\times$ 0.7 μ.

Hysterographium Mori (Schw.) Rehm

No. 213. On decorticated limbs of *Rhus typhina* L., Ann Arbor, Mich., May 1, 1930. No. 2. On decorticated trunk of *Ulmus fulva* Michx., Ingham County, Mich., Oct. 14, 1928. No. 6. On decorticated limbs of *Ulmus americana* L., Ann Arbor, Mich., Nov. 15, 1928. No. 32. On decorticated, much-weathered trunk, *Fraxinus sp.*, Ann Arbor, Mich., Nov. 15, 1928. No. 7. (originally identified as *H. cinerascens* (Schw.) E. & E.). On decorticated, weathered limbs of *Ulmus americana* L., Ingham County, Mich., Oct. 14, 1928. All collections by M. L. Lohman.

This common species has been collected in abundance in its various forms and intergrading types. The collections show the species to be as variable as Ellis (12, p. 704) has indicated. The writer's decision to relegate *Hysterographium cinerascens* (Schw.) E. & E. to the *H. Mori* group adds to the complexity in that Schweinitz (44, p. 244) described *H. cinerascens* first. Since there is some disagreement concerning the type material of *H. cinerascens* Schw., the writer prefers to employ the name in common use.

Vegetative cultural characteristics. — The strains already mentioned showed no differential characters on the media utilized. All produced a white mycelium, which soon became a persistent gray ("olive-gray") or greenish gray ("tea green"). Mycelia grew at a moderate rate and produced irregularly convoluted

and lobed surface mats 2 to 4 mm. deep, with a very thin superficial layer of delicate hyphae.

Cultural fructifications. — Pycnidiospores are produced in irregular cavities within the surface layer (Fig. 40 *B*). Centers of pycnidiospore production are noticeable in old cultures as erect

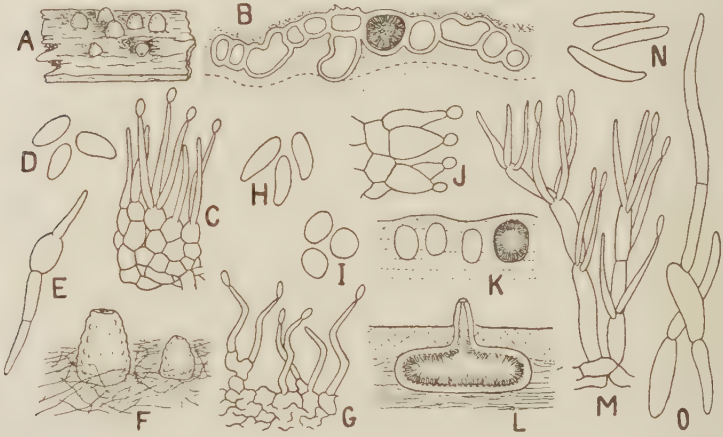

FIG. 40. *A–E, Hysterographium Mori. A*, pycnidia on wood, × 20; *B*, pycnidial cavities in the surface layer on agar media (the three culture layers are indicated); *C–D*, sporulating cells and pycnidiospores; *E*, germinating pycnidiospores; *C–E*, for field material and cultures. *F–H, Hysterographium vulvatum;* pycnidial stage obtained in culture. *F*, pycnidia, × 75; *G–H*, spore-bearing cells and pycnidiospores. *I–K, Hysterographium formosum;* pycnidial stage obtained in culture. *I–J*, pycnidiospores and spore-bearing cells; *K*, cavities in surface layer on agar medium. *L–O, Hysterographium Fraxini;* pycnidial stage from cultures on sterilized ash twigs. *L*, section view of pycnidium within the bark, × 40; *M–N*, spore-bearing cells and pycnidiospores; *O*, germinating pycnidiospores

tufts of white delicate hyphae produced by subsequent upward growth of the hyphae, which differentiate the walls of the cavities, and by the germination of exuded pycnidiospores under moist culture conditions. The wall is brown, small-celled parenchymatous, and measures 10 to 15 μ in thickness. The simple sporulating cells are 8–10 × 1.5–2 μ and abstrict the hyaline pycnidiospores singly from their tips. These spores are elliptic-inequilateral to ovate and measure (2) 2.5–3.5 (4) × (0.7) 1–2 μ.

Observed associations. — A pycnidial stage (Figs. 40 *A*, *C–E*) of the Aposphaeria type is commonly associated with all the forms given above. The pycnidia are erumpently superficial, 100 to 125 μ in diameter, and usually precede and border the aggregations of hysterothecia. The hymenial elements are identical with those obtained in culture. The pycnidia arise within the wood or as cavities in the thin, black crust, with their basal walls poorly developed at first. But the blackened, subcarbonaceous wall is complete in mature pycnidia. This stage is usually more abundant in material referable to *H. cinerascens*, since the numerous minute pycnidia are largely responsible for the ashy coloration of the wood.

Hysteropycnis admixta and *H. confluens* (see pp. 232-233), recently described by Hilitzer (18, p. 152) as associated with *Hysterographium Dubyi* Hilitzer and *H. elongatum* Corda, respectively, are probably pycnidial stages very similar to that associated with *H. Mori*.

Hysterographium Lesquereuxii (Duby) Sacc.

No. 11. On decorticated limbs of *Acer saccharinum* L., Ann Arbor, Mich., Oct. 20, 1928. Collected by M. L. Lohman. This material is tentatively referred to *H. Lesquereuxii*.

The cultures of this fungus showed constant slight differences from cultures of all forms of *H. Mori*. As compared with the latter cultures, the mycelia remain lighter in color with a tinge of yellow, the oatmeal is discolored yellow and then olive-brown at room temperature, the superficial weft is deeper, broadly zoned, and crenately lobed on the margin, and pycnidiospores are produced in greater abundance. The pycnidial stage, in culture and on collected material, is indistinguishable from that of *H. Mori*.

In spite of the differences in cultural characteristics and spore markings the material tentatively referred to *H. Lesquereuxii* (Duby) Sacc. is probably only another form of *H. Mori*.

Hysterographium formosum (Cooke) Sacc.

No. 245. On fallen twigs of *Pinus albicaulis* Englem., Crater Lake National Park, Ore., Sept. 10, 1929. Collected by L. N. Goodding.

Hysterothecia as described by Ellis (12, p. 702); asci 100–130 × 10–12 μ; spores 18–21 × 7–8 μ. The material agrees with the type "*1020. Hysterium formosum* Cooke," at Kew.

This western species will probably be found to be identical with the European *H. Pumilionis* Rehm (36, p. 21), which, according to Rehm (38, p. 109), is common on dead twigs of Pinus in alpine regions.

The spores of *H. formosum* germinate at 20 to 25° C., but the organism demands low temperatures for vigorous vegetative growth. When subcultures on the Leonian medium from vigorous mycelia at 10° C. were placed at room temperature, there was a transformation of the mycelium into a compact sclerotial mass, but new hyphae scarcely penetrated the medium. Such transfers showed no appreciable growth in eight weeks, whereas cultures of the same duration at 10° C. developed a mycelial weft 2 cm. in diameter. At eight weeks a set of the former cultures was removed to 10° C. and vigorous mycelial development followed.

Vegetative cultural characteristics. — Growing mycelium (in this case on sucrose oatmeal at 10° C.) is black and forms a smooth surface layer suggesting *Hysterium pulicare*, but a gray-green superficial layer develops tardily. At 20 to 25° C. the sclerotic bodies are dark brown, owing to the production of numerous, intercalary or terminal, globose resting cells, which are occasionally septate.

Cultural fructifications. — Pycnidiospores are produced in abundance at 10° C. on the oatmeal medium. The rather regular, spherical cavities (Fig. 40 *I*), 150 250 μ in diameter, are developed in clusters within the surface layer. The spores escape and form on the surface irregular, firm, white mucilaginous concretions. The pycnidiospores are subglobose to short-oblong, 2 μ in diameter or 2.5 × 2 μ, and they are abstricted from inverse-pyriform sporulating cells 4 to 6 μ in length (Fig. 40 *J–K*). It is to be noted that these spores and spore-bearing cells are of the type described for *Mytilidion tortile*.

Hysterographium vulvatum (Schw.) Rehm. (Pl. XXXV, Fig. 1)

No. 4. On decorticated twigs of *Quercus alba* L., Ann Arbor, Mich., Nov. 13, 1928. Collected by M. L. Lohman.

The variability in hysterothecial development and spore size encountered in this large-spored Hysterographium, common about Ann Arbor on the bark and decorticated areas of dead twigs of Quercus, suggests that the names *Hysterium flexuosum* Schw. (43, p. 49) and *H. vulvatum* Schw. (44, p. 243) probably apply to the same organism. In Ann Arbor collections the spores measure (45) 50–58 (65) × (12) 14–18 (22) μ.

In its vegetative cultural characteristics *H. vulvatum* resembles *H. kansense,* except that the superficial layer is a darker green.

Cultural fructifications. — Pycnidiospores appear in large quantities on the oatmeal medium. Hymenial tissue is developed upon the surface layer without cavity formation, and the masses of spores are soon covered by superficial, delicate hyphae. The pycnidiospores are hyaline, acrogenetic, oblong-inequilateral, and measure 3–4 × 1.3–1.5 μ. The sporulating cells measure 5–8 × 1.5 μ. They are variously bent and arise singly from a loose tissue of delicate, much-branched hyphae (Figs. 40 *G–H*). Ostiolate pycnidia (Fig. 40 *F*) 75 to 90 μ in diameter and 100 to 150 μ in height were produced in the aërial mycelium of certain granulated cork cultures. These pycnidia had membranous walls 6 to 8 μ thick, including the loose subhymenium, and hymenial elements as described for the cultures on oatmeal. The surface layer on the oatmeal medium contains numerous, one- or several-celled, brown chlamydospores.

Hysterographium Fraxini (Pers. ex Fr.) De Not.

No. 300. On bark, fallen twigs of *Fraxinus pennsylvanica* Marsh., Manitoba Agricultural College Grounds, Winnipeg, Canada, Sept. 17, 1930. Collected by Professor G. R. Bisby.

H. Fraxini was collected at Ann Arbor in 1895, but it has not been reported since that date. It is one of the classic species of the group.

Vegetative cultural characteristics. — The spores germinate by a number of abruptly branched, septate, coiled and interwoven hyphae (31). Mycelial growth is white, as Brefeld (3, p. 271) noted, and where a superficial layer is developed, as on the oatmeal medium, it remains white until the third or fourth month.

On the cork-decoction medium the superficial layer is lacking, and the culture is dark brown. A scant, superficial, white mycelium is produced on sterilized ash twigs. On agar media the hyphae secrete a mucilaginous substance in great amounts, giving elastic properties to the tough mycelial wefts.

Cultural fructifications. — Drops from one capsule of sterile distilled water containing spores in suspension were placed upon nutrient agar plates and upon steam-sterilized ash twigs. From the nutrient plates a number of single-spore and single-ascus isolations were made. When growth from these isolations permitted, transfers were made to steam-sterilized ash twigs, to cork-decoction media, and to fresh bark wounds on dormant ash twigs in the laboratory. By the fourth week the sterilized twigs that had been inoculated with a mass of germinating ascospores showed scattered olive-green spore horns. Observation at the end of the fourth month revealed that pycnidia had not been formed in any single-spore and single-ascus culture on the agar media, nor on dormant or steam-sterilized ash twigs that had been inoculated from such cultures. Uninoculated steam-sterilized twigs remained sterile.

The pycnidia (Fig. 40 *L–O*) which were responsible for the spore horns noted above are intracorticular, 500 to 600 μ in diameter and 200 to 270 μ in height, exclusive of the protruding ostiolate papillae, and they have complete, small-celled, clear-brown, parenchymatous walls averaging 25 μ in thickness. The pycnidiospores are hyaline, cylindric-bent to allantoid, and measure 4.5–5 $\times$ 0.8–1.2 μ. The spore-bearing cells measure 8–12 $\times$ 1–2 μ, but they arise in irregular clusters from a thicker, septate, central hypha. If the latter is considered the conidiophore, the pycnidial stage is referable to Dendrophoma Sacc. in the systems of Von Höhnel (20) and Diedicke (8), or possibly to Ceratophoma in the system of Von Höhnel.

A pycnidial stage with more superficial fructifications, but with similar spores, has been described for this species as *Hysteropycnis Fraxini* Hilitzer (18, p. 152).

A stylosporic stage (see p. 232), as described by Rostrup (40) and referred by Lind (26) to the form genus Myxosporium, has

not been observed by the writer, in cultures or in collected material.

Observed associations. — The source material shows an intracorticular pycnidial stage, but the pycnidia are considerably smaller than those obtained in culture, and they are without hymenial elements.

Gloniopsis brevisaccata Lohman, sp. nov. (Pl. XXXIV, Fig. 3)

Hysterotheciis 0.6–0.8 (1) mm. longis, 0.15–0.25 mm. latis, atris, rugosi-punctatis, lineari-oblongis, superficialiter erumpentibus sed sursum complanatis, rimis longitudinalibus et striis parallelis obscuris, dense longiseriatis secus ligni interstitia, textura carbonaceis, parenchymatosis cum loculis minutis; ascis breviter clavatis, octosporis, 65–75 μ longis, 15–21 μ crassis; paraphysibus filiformibus, sparsis, septatis, supra ramosis et intertextis, epithecium fuligineum formantibus; sporidiis hyalinis, indistincte merenchymatosis, subtristichis vel inordinate distichis, 28–30 (35) × (10) 12–14 μ, leviter curvatis, 7- vel 10-septatis, septo medio quam ceteris validius constricto, utroque obtusis.

Habitat superne in trunco erecto vetusto querceo. Ann Arbor, Mich., Nov. 15, 1928. Specimen typicum in herb. Univ. Mich.

Hysterothecia 0.6–0.8 (1) × 0.15–0.25 mm., linear-oblong, flattened, rugose-punctate, erumpently superficial, densely gregarious, in long linear series following the interstices of the wood, each with a few faint striae paralleling the shallow longitudinal fissure; walls carbonaceous, rather thin but small-celled parenchymatous; asci short-clavate, double-walled, 65–75 × 15–21 μ; paraphyses sparse, slender, septate, branched and interwoven above to form a brownish epithecium; spores hyaline, curved with obtuse ends, subtriseriate to biseriate, 28–30 (35) × (10) 12–14 μ, 7 to 10 cross-septate, deeply constricted at the central septum and less so at the primary septum of each half, indistinctly merenchymatous by a number of longitudinal divisions.

Near top of standing fence post (Quercus); Ann Arbor, Mich., Nov. 15, 1928. Collected by M. L. Lohman (No. 25). Type in the herbarium of the University of Michigan.

The fungus was again collected from the same post on September 18, 1930. The minute hysterothecia and the large spores in

short, thick asci are the distinctive characteristics. In respect to the latter the fungus approaches *G. decipiens* De Not. (6, p. 23; cf. Rehm 36, p. 18). The material was tentatively referred to *Hysterium lineolatum* as described by Cooke (Grev., 11 : 107. 1883) — not *Hysterographium praelongum* (Schw.) E. & E., Ellis 1321 (North Am. Fungi) — but an examination of the type material from Cooke's herbarium indicated that the writer's material cannot be referred to Cooke's species, which, perhaps, should be transferred to the genus Tryblidaria. Incidentally, the type materials indicate clearly how Ellis (12, p. 708) came to err in regarding the names *Hysterium lineolatum* Cooke and *H. praelongum* Schw. as synonyms.

Vegetative cultural characteristics. — The organism is distinguished from *Glonium simulans* by the persistently lighter color of the aërial mycelium and a fainter discoloration of the oatmeal medium. In old cultures it produces the erect dendroidal tufts noted for *Hysterographium minutum*. These tufts presented aërial pycnidial primordia, but sporulation was not observed.

Gloniopsis Gerardiana Sacc.

No. 5. On decorticated limb of *Ulmus americana* L., Ann Arbor, Mich., Nov. 15, 1928. Collected by M. L. Lohman.[7]

Cultures of this species differ from those of *H. Mori* in that they are lighter in color, the superficial layer is thinner and more compact, and primarily in that concentric zonations and symmetrical radial folding are constant characteristics.

Cultural fructifications. — Pycnidiospores were produced in abundance, and this stage could not be distinguished from that obtained culturally for *H. Mori*.

Observed associations. — Pycnidial accompaniment is more frequent in collections of this species than in those of *H. Mori*. Pycnidia (Fig. 40 *A*) of the two species are not satisfactorily distinguished by morphological characteristics.

[7] This is *Hysterographium gloniopsis* (Ger.) E. & E. as described by Ellis (12, p. 708). The validity of his synonymy has not been verified. In the original material for cultures the asci measure 55–60 × 10 μ and the spores 15 × 5–6 μ. In other details the spores agree with those described by Ellis (*op. cit.*) and by Gerard (17, p. 78).

Hysteropatella Prostii (Duby) Rehm

No. 144. On bark and wood of fallen twigs, *Fraxinus pennsylvanica* Marsh., Randolph County, Ind., Sept. 17, 1929. Collected by M. L. Lohman.

Rehm (36, pp. 301, 367; 38, p. 104) studied this species more fully than any other student of the group. Ellis (12, p. 697) and Seaver (45, p. 112) have described American material.

Vegetative cultural characteristics. — Developing mycelia are black and form a smooth surface layer. Cultures are distinguished from those of *Hysterium pulicare* by the pycnidial stage, which is more erumpent and of earlier appearance.

Cultural fructifications. — Pycnidial primordia arise singly or clustered within the surface layer. Clustered primordia develop a compound fructification. Mature fructifications (Fig. 41 *A*) are slightly erumpent from the surface layer and measure 75 to 100 μ in diameter and 100 to 200 μ in height. The wall is thin, complete, and small-celled parenchymatous. The spore-bearing cavities may coalesce through the dissolution of intervening tissue, or the coalescence may occur only apically, which results in a labyrinthiform central portion. Fructifications of the latter type have a broad opening above which is surrounded by a thick palisade of delicate hyphae. The hymenium consists of irregularly clustered sporulating cells measuring 8–12 × 1.5–2 μ, and of thicker, septate, long-tapering sterile hyphae. The pycnidiospores (Figs. 41 *B C*) are acrogenetic, hyaline, elongate, slightly curved, and measure 3–4.5 × 1–1.5 (2) μ. These spores were germinated, and the development of septate, branching hyphae from individual spores was observed (Fig. 41 *D*).

Hysteropatella clavispora (Peck) Seaver

No. 143. On inner bark at storm break, *Salix sp.*, Randolph County, Ind., Sept. 17, 1929. Collected by M. L. Lohman.[8]

[8] When Seaver (45, p. 113) transferred *Tryblidium clavaesporum* Peck (33, p. 143) to the genus Hysteropatella, he listed *Patellaria clavispora* (Peck) Sacc. (*Syll. Fung.*, 8:787) as a synonym of the new combination, but he failed to include *Tryblidiella clavispora* (Peck) Berl. & Vogl. (*Syll. Fung.*

Vegetative cultural characteristics. — Mycelial growth is confined to the medium. This results in a smooth surface layer, as noted under *H. Prostii.* Cultures of this species, however, are sordid white to yellowish brown and become black only on standing for several months. The blackening appears as pycnidial production begins. Cultures producing pycnidia in abundance

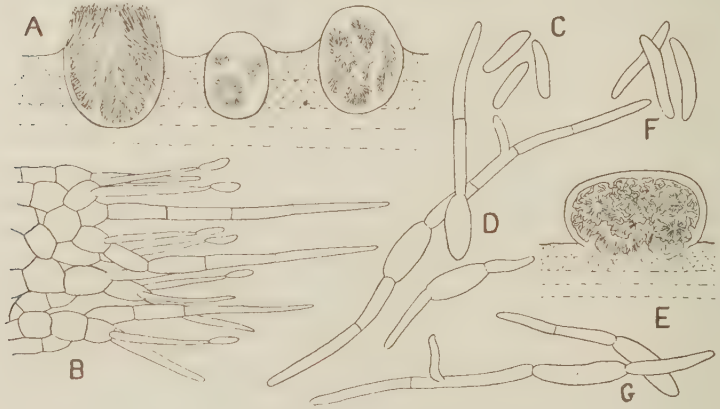

FIG. 41. *A–D, Hysteropatella Prostii;* pycnidial stage from cultures. *A*, sectional view of fructifications in surface layer on agar medium, × 150; *B–C*, spore-bearing cells and pycnidiospores; *D*, germinating pycnidiospores. *E–G, Hysteropatella clavispora;* pycnidial stage from cultures. *E*, immature fructification on agar medium, × 50; *F*, pycnidiospores; *G*, the same, germinating

are entirely black and are distinguishable from those of the preceding species and those of *Hysterium pulicare* by the more numerous exuded masses of pycnidiospores.

Cultural fructifications. — The pycnidial stage (Figs. 41 *E–G*) obtained in culture corresponds in its general type to that described for the preceding species. Compound fructifications are larger, measuring 300 to 400 μ in diameter and 150 to 200 μ in height. The pycnidiospores of this species are more elongated,

Addit. 1–4, p. 267), which also becomes a synonym. Rehm (37) did not include this species in his revision of Tryblidium and Tryblidiella. The description given by Ellis (12, p. 690) is adequate for my material.

measuring 4–5 (6.5) × 0.9–1.5 (2) μ, and they are definitely allantoid to subsigmoid. They are exuded in greenish yellow masses rather than in the sordid white globules of the preceding species. They show under magnification a more dense, protoplasmic content, which occasionally appears two-parted at the time of germination. Mycelial development from germinating pycnidiospores was also observed in this species.

GENERAL CONCLUSIONS

1. The results of the studies indicate that apparently only a few of the species of the carbonaceous, hysteriaceous fungi have hyphomycetous imperfect stages.

Since these studies establish a Papulospora stage for *Lophium mytilinum* (Pers.) Fr. and a Septonema stage for *Hysterium insidens* Schw., supposedly an American species, similar stages might be sought respectively in connection with the European forms of the former species and with the European *H. Berengerii* Sacc., which is similar to *H. insidens* in its habit and morphology.

2. The pycnidial ("spermatogonial") fructifications, with their minute pycnidiospores ("spermatia"), do show specific differences, as evidenced by the three types of secondary spores (Table II).

This situation contradicts Duby's (9, p. 27) conception of the worthiness of such studies in this group and supports Rehm's (36, p. 3) anticipations that a study of the imperfect stages might possibly make clearer the position and limitation of species in this group. Among the nineteen species for which a pycnidial stage is described in this report only *Hysterographium Mori* (Schw.) Rehm, *H. Lesquereuxii* (Duby) Sacc., and *Gloniopsis Gerardiana* Sacc. present both in culture and in field material pycnidial stages which cannot be satisfactorily distinguished.

3. Secondary spore stages are expressions of particular potentialities of the fungus, and the form of their reproductive cells is constant, within limits. They cannot be ignored, therefore, if our conception of specific relationships is to be founded upon the full biology of the organism concerned.

The similarity of the pycnidial stages of *Glonium parvulum*

TABLE II

SYNOPSIS OF LIFE-HISTORIES PRESENTED *

Species	Imperfect stages	Pycnidiospores	
		Type	Germination
LOPHIUM			
L. mytilinum	Papulospora mytilina (c, a) and pycnidial near Dothiorella (c, a)	II	c, a
GLONIUM			
G. stellatum	Sphaeronaema byssoideum (a)	II	
G. parvulum	Sphaeronaema parvulum (c, a)	II	c
G. lineare	Plenodomus-Dothiopsis-Phomopsis group (c, a)	II	
MYTILIDION			
M. tortile	Pycnidial (c), undetermined	I	
M. decipiens	Hyphomycetous (c), undetermined		
	Pyrenochaeta-Sclerochaeta ? (c)	I	
M. resinicola	Aposphaeria ? (a)	I	a
M. Thujarum	Pycnidial near Aposphaeria (a)	I ?	
HYSTERIUM			
H. pulicare	Pycnidial (c, a), undetermined	III	c, a
H. insidens	Septonema spilomeum Berk. (c, a)		
	Pycnidial (c, a), undetermined	III	c
HYSTEROGRAPHIUM			
H. minutum	Aposphaeria ? (a)	III	
H. Mori	Aposphaeria (c, a)	II	c, a
H. Lesquereuxii	Aposphaeria (c, a)	II	
H. formosum	Pycnidial (c), undetermined	I	
H. vulvatum	Pycnidial (c)	III	
H. Fraxini	Dendrophoma-Chaetophoma (c)	III	c
GLONIOPSIS			
G. Gerardiana	Aposphaeria (c, a)	II	c
HYSTEROPATELLA			
H. Prostii	Pycnidial (c), undetermined	III	c
H. clavispora	Pycnidial (c), undetermined	III	c

* Imperfect stages were not discovered for the following species: *Lophium dolabriforme, Glonium simulans, Mytilidion laeviusculum, Hysterium angustatum, Hysterographium kansense,* and *Gloniopsis brevisaccata.*

For explanation of letters and roman numbers see bottom of opposite page.

(Ger.) Cooke and *G. stellatum* Muhl. suggests a reasonable intrageneric relationship and is not favorable to the adoption of Psiloglonium v. H. with generic ranking on the basis upon which it was founded by Von Höhnel (19) and emended by Petrak (34). Also, when species have been described (*Hysterium cinerascens* Schw., *H. Mori* Schw., *H. Rousselii* De Not., and *H. Gerardi* C. & P.) and later found to lack diagnostic characters of value and to possess identical secondary spore stages, a broadening of the species concept is most feasible.

4. An appreciation of the real significance of our knowledge of the life-histories of these species, in relation to their generic positions, must await the determination of imperfect stages in a sufficiently large number of the species.

5. For the purpose of comparison the size and form of the pycnidiospores and the cells from which they originate are more reliable than characters pertaining to the tissue which supports them, whether the cultural fructification or field material is being considered.

6. Vegetative cultural characters alone are distinctive and might possibly aid in the classification of species which show intermediate generic characters in the morphology of the hysterothecium.

In the past Mytilidion has been distinguished from Hysterium primarily by the form of the hysterothecium. The thickness and hyphal structure of the wall, criteria which have not been emphasized by previous workers, are of greater importance. *Mytilidion Thujarum* (C. & P.) Lohman is intermediate between Hysterium

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EXPLANATION OF LETTERS AND ROMAN NUMBERS USED IN TABLE II

c — obtained in culture
a — associated with perfect stage in field material

I — pycnidiospores spherical to subglobose; spore-bearing cells usually minute, obovate, and difficult to discern
II — pycnidiospores ovate-inequilateral to oblong-elliptic; spore-bearing cells usually slender-clavate
III — pycnidiospores elongate-cylindric and suballantoid or subsigmoid; spore-bearing cells slender-clavate and usually longer than in group II

The form of the pycnidium and the development and the texture of the wall vary in each of the three groups.

and Mytilidion in that the hysterothecia are not truly conchiform, but do possess thin walls of a prosenchymatous structure characteristic of conchiform hysterothecia. In its cultural characters the fungus resembles certain species of Mytilidion.

7. In determining the affinities of the family the value of a knowledge of secondary spore stages will be manifoldly increased when a similar knowledge has been made available for the Lophiostomataceae and for certain genera of the Patellariaceae, the Tryblidiaceae, and the Graphidaceae.

Life-history studies in these various forms and in the Hypodermataceae will probably yield evidence in support of Von Höhnel's (19) disposition of the species of the old order, just as the cultural studies by Wehmeyer (46) on certain species of the stromatic Sphaeriales supported, in general, Von Höhnel's revisions of that group.

SUMMARY

A physiological study involving single-spore and single-ascus cultures of carbonaceous, hysteriaceous fungi, intended to derive some information that might supplement the morphological characters in the taxonomy of the species, has resulted in the isolation and comparative cultural study of twenty-two known species and three apparently heretofore undescribed forms. *Gloniopsis brevisaccata*, *Hysterographium minutum*, and *Mytilidion resinicola* are described in this paper as new species.

The cultural studies have indicated that in general the species are distinct in their vegetative characteristics and that fifteen of the twenty-five species produce secondary spore stages in culture. In three of the species that remained sterile in culture a pycnidial stage was observed as associated with the perfect stage in field material and accepted in each case as belonging to the known perfect stage because imperfect stages of similar type had been obtained in cultures of closely related species.

Three species possess hyphomycetous stages: *Lophium mytilinum* (Pers.) Fr., with a Papulospora type for which the name *P. mytilina* is suggested; *Mytilidion decipiens* (Karst.) Sacc., with an unidentified mucedinaceous stage; and *Hysterium insidens* Schw., with a Septonema stage determined as *S. spilomeum* Berk.

Lophium dolabriforme Wallr. develops catenulate filaments in culture, but they are not definitely interpreted as a form of conidial reproduction.

For nineteen of the species some information has been obtained concerning the pycnidial stages. These stages are described in detail and most of them are figured. All show hyaline, one-celled pycnidiospores. Three types of pycnidiospores are recognized: (1) spherical to subglobose and typically produced on minute, obovate, spore-bearing cells; (2) ovate-inequilateral to oblong-elliptic and typically produced on slender, clavate, spore-bearing cells; and (3) elongate or cylindric, straight, suballantoid to subsigmoid, and produced on elongate-clavate, spore-bearing cells, many of which are accompanied by sterile filaments. *Mytilidion tortile* (Schw.) Sacc., *M. decipiens* (Karst.) Sacc., *Mytilidion resinicola* Lohman, sp. nov., *M. Thujarum* (C. & P.) Lohman, comb. nov., and *Hysterographium formosum* (Cooke) Sacc. show pycnidial stages of the first type. *Lophium mytilinum* (Pers.) Fr., *Glonium stellatum* Muhl., *G. parvulum* (Ger.) Cooke, *G. lineare* (Fr.) De Not., all the forms of *Hysterographium Mori* (Schw.) Rehm, *H. Lesquereuxii* (Duby) Sacc., and *Gloniopsis Gerardiana* Sacc. give pycnidial stages of the second type. *Hysterium pulicare* Pers. ex Fr., *H. insidens* Schw., *Hysterographium vulvatum* (Schw.) Rehm, *H. Fraxini* (Fr.) De Not., *Hysterographium minutum* Lohman, sp. nov., *Hysteropatella Prostii* (Duby) Rehm and *H. clavispora* (Peck) Seaver compose the third group.

The pycnidial stages of *G. parvulum* and *G. stellatum* are referred to the form genus Sphaeronaema, as *S. parvulum* Lohman, status novus, and *S. byssoideum* Lohman, status novus, respectively. The pycnidial stages of *Hysterographium Mori*, *H. Lesquereuxii*, and *Gloniopsis Gerardiana* are of the form genus Aposphaeria. They are not satisfactorily distinguished. The pycnidial stage of *M. resinicola* might be referred to the same form genus, but its pycnidiospores are subglobose.

Although these spores average less than 2 μ in diameter and the elongate forms seldom exceed 6 μ in length, they are referred to as pycnidiospores and their fructifications as pycnidia because the spores have been germinated and hyphal development has

been observed in the following species: *Glonium parvulum, Lophium mytilinum, Mytilidion resinicola, Hysterium pulicare, H. insidens, Hysterographium Fraxini, H. Mori, Gloniopsis Gerardiana, Hysteropatella Prostii,* and *H. clavispora.* Single germinating pycnidiospores of *L. mytilinum, G. parvulum,* and *H. insidens* were isolated, and the pycnidiospores produced mycelia similar to those of ascospore cultures in the respective species, and in each species returned the pycnidial stage in culture.

As a result of the observations on field material and in view of comparative cultural data, the following revisions in the taxonomy of the family are made: *Hysterium Thujarum* C. & P. is transferred to the genus Mytilidion; *Hysterographium cinerascens* (Schw.) E. & E. is considered only a form of *H. Mori* (Schw.) Rehm. Also, there is evidence that the genus Psiloglonium Petrak is apparently not well founded.

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University of Michigan

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EXPLANATION OF PLATES XXXIV–XXXV

(All materials are illustrated twice the natural size.)

PLATE XXXIV

FIG. 1. *Mytilidion tortile* (Schw.) Sacc., on bark of living *Juniperus virginiana* L.; the minute, scattered, subflexuous, acutely ridged and irregularly oriented fructifications are distinctive.

FIG. 2. *Mytilidion Thujarum* (C. & P.) Lohman, comb. nov. (*Hysterium Thujarum* C. & P., *Bull. Buffalo Soc. Nat. Sci.*, p. 33. 1875), on bark of old stumps, *Thuja occidentalis* L.

FIG. 3. *Gloniopsis brevisaccata* Lohman, sp. nov., on much-weathered, standing post (Quercus).

FIG. 4. *Glonium simulans* Ger., on decorticated wood of *Tilia americana* L.; note the blackened condition of the wood and the obtuse ends of the hysterothecia.

FIG. 5. *Glonium stellatum* Muhl. (*Sphaeronaema byssoideum* Lohman, status novus *Glonii stellati*), on much-decayed Quercus log; note the minute, scattered, beaked pycnidia.

PLATE XXXV

FIG. 1. *Hysterographium vulvatum* (Schw.) Rehm, on a weathered, fallen branch of *Quercus alba* L.; the several longitudinal striations which parallel the central fissure are unusually prominent in the material of this collection.

FIG. 2. *Hysterographium kansense* E. & E., on bark of living *Quercus alba* L.; easily mistaken for *Hysterium pulicare* Pers. ex Fr. until examined microscopically; the hysterothecia are slightly more robust than those of *H. pulicare*.

FIG. 3. *Hysterium insidens* Schw. (*Septonema spilomeum* Berk., *London Journ. Bot.*, 4 : 310. 1845), on much-weathered paling (Quercus) of old and dilapidated picket fence; note (central portion and upper right) the circular, erumpent, weathered fructifications of the Septonema imperfect stage.

PLATE XXXIV

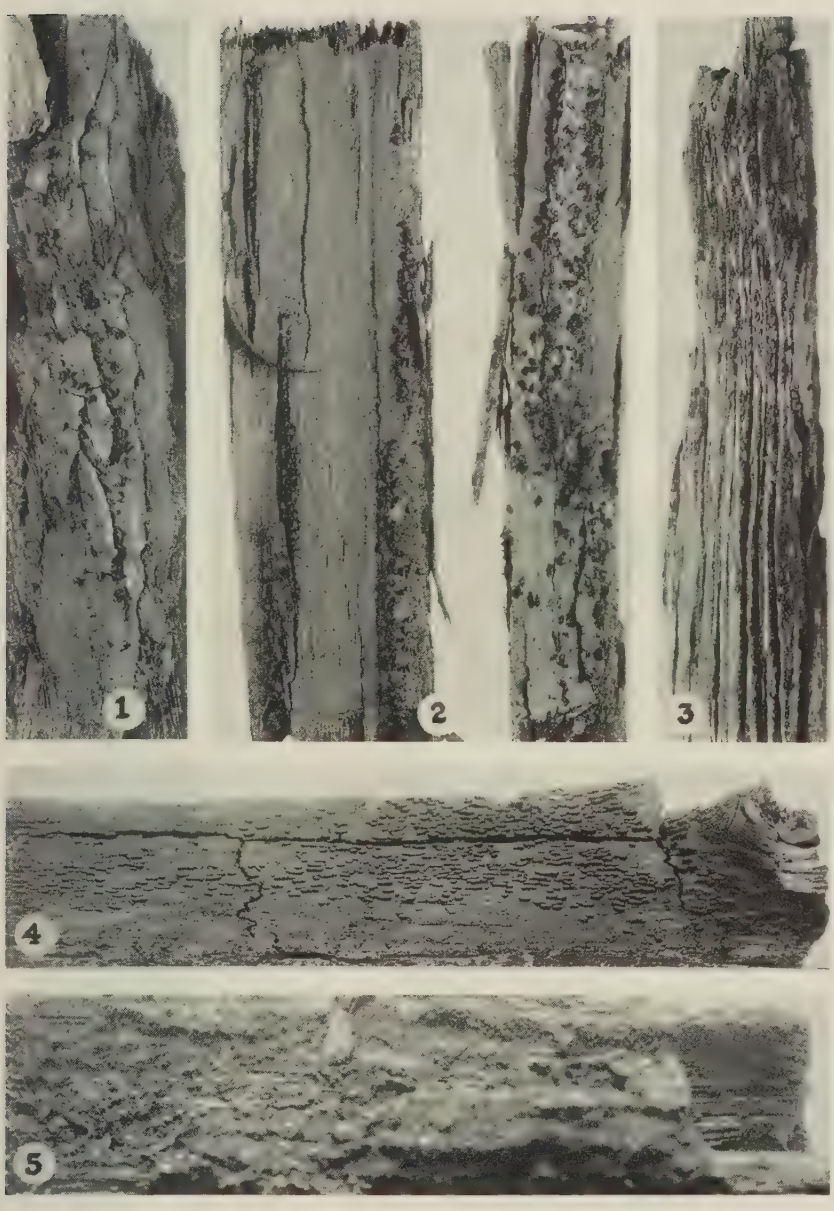
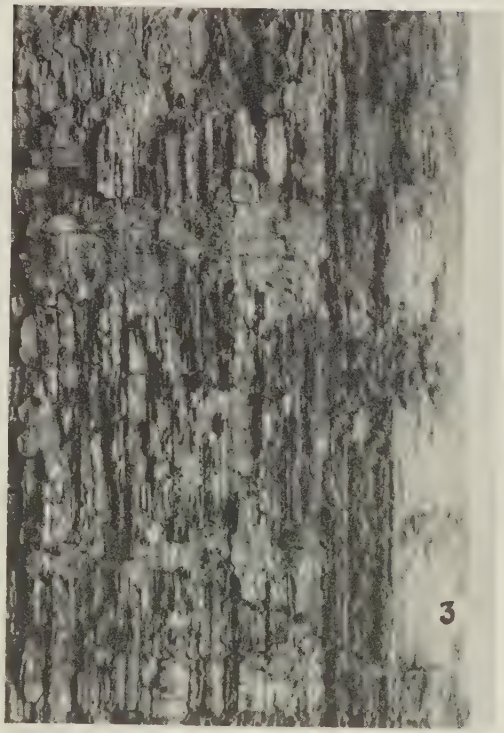
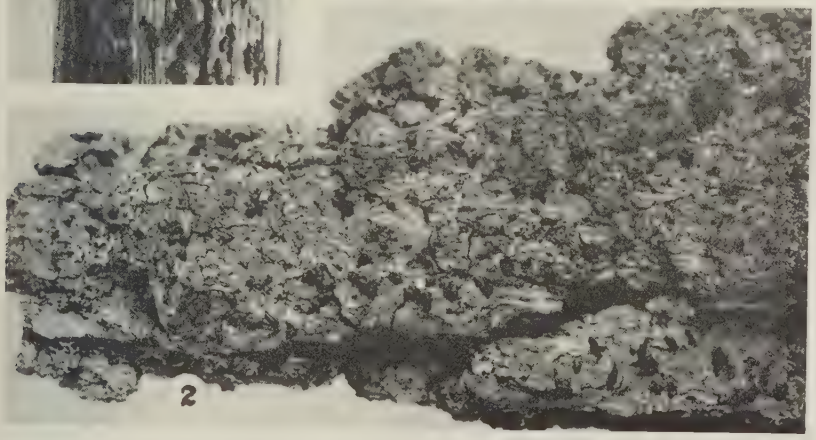


PLATE XXXV





HOST SPECIALIZATION IN THE LEAF RUST OF GRASSES, *PUCCINIA RUBIGO-VERA* *

EDWIN B. MAINS

I. Introduction

IT IS proposed in this paper to discuss the host specialization of a group of rusts of which the leaf rust of wheat (*Puccinia triticina* Erikss.) is typical. These rusts are characterized by scattered uredinia containing ellipsoid or subgloboid urediniospores having 8–10 scattered germ pores. The telia are scattered and are long covered by the epidermis of the host. The teliospores are closely packed together in the telium, which is bordered by a more or less well developed layer of closely packed brown paraphyses, sometimes considered a stroma.

The nomenclature of these rusts is somewhat involved. De Candolle (1815) described a rust occurring principally on wheat under the name *Uredo rubigo-vera* DC. Winter (1884) placed this in Puccinia under the name *Puccinia rubigo-vera* (DC.) Wint. Winter states that this species is found on different grasses and lists species of Cynoglossum, Borago, Anchusa, Lycopsis, Nonnea, Symphytum, Cerinthe, Echium, Pulmonaria, and Lithospermum as aecial hosts. The assignment of these boraginaceous hosts to this species was probably based on the studies of De Bary (1867), who had connected the leaf rust of rye with aecia on *Anchusa officinalis* and *Anchusa* (*Lycopsis*) *arvensis*. Winter considered the leaf rust on species of Hordeum a variety under the name *Puccinia rubigo-vera simplex* Körnicke.

* The investigations upon which this study is based were made while the writer was at Purdue University and were part of the coöperative investigations by the Purdue Agricultural Experiment Station and the Office of Cereal Investigations of the United States Department of Agriculture. Papers of the Department of Botany No. 390 and the University Herbarium, University of Michigan.

Winter gives *Puccinia striaeformis* Westend. and *Puccinia straminis* Fuckel as synonyms. Westendorf (1854) described *Puccinia striaeformis* as having long-covered telia. He states that the pustules were at first scattered and then confluent, to form continuous longitudinal lines several centimeters long. Fuckel (1860) also described a rust of cereals having long-covered telia which were confluent in lines. He considered *Uredo rubigo-vera* DC. a synonym. The descriptions would indicate that these rusts are different from *Uredo rubigo-vera* DC.

The concept of *Puccinia rubigo-vera* as a species prevalent on a number of grasses has been held by various mycologists. Thus De Toni (1888) lists species of Anchusa, Pulmonaria, Symphytum, Borago, Cynoglossum, Lycopsis, Nonnea, Cerinthe, Echium, and Lithospermum as the aecial hosts and species of Alopecurus, Agrostis, Polypogon, Calamogrostis, Triticum, Secale, Holcus, Avena, Bromus, Milium, Koeleria, Trisetum, Scleria, Festuca, Elymus, and Lagurus as hosts for the uredinia and telia. Plowright (1889) gives *Anchusa arvensis* and *Echium vulgare* for the aecial hosts and *Bromus mollis, Triticum vulgare, T. repens, T. sativum, Secale cereale, Hordeum vulgare, Holcus lanatus, H. mollis, Avena sativa,* and *A. elatior* for the uredinia and telia.

Schroeter (1889) lists *Anchusa officinalis, A. arvensis, Symphytum officinale, Borago officinalis, Pulmonaria officinalis* as aecial hosts and *Alopecurus pratensis, Agrostis vulgaris, Calamagrostis epigea, Milium effusum, Koeleria aurea, Trisetum flavescens, Festuca pseudomyurus, F. silvatica, Bromus secalinus, B. mollis, B. arvensis, B. asper, B. sterilis, B. tectorum, Triticum vulgare, T. repens, T. caninum, Elymus europaeus,* and *Secale cereale* for the hosts of the uredinia and telia.

Oudemans (1893) gives *Cynoglossum officinale, Lycopsis arvensis, Symphytum officinale* for the aecial hosts, and *Agropyron repens, Arrhenatherum elatius, Bromis mollis, B. tectorum, Holcus mollis, Hordeum secalinum, H. vulgare, Phragmites communis, Secale cereale,* and *Triticum vulgare* for uredinia and telia.

The name *Puccinia rubigo-vera* was applied, in the United States, to the leaf rust of some of the cereals by Burrill (1885), Bolley (1889), Hitchcock and Carleton (1893, 1894), Carleton

(1899), and Freeman and Johnson (1911). Carleton, followed by Freeman and Johnson, recognized two races separable by host specialization, that on wheat being designated as *Tritici* and that on rye, *Secalis*.

Apparently the idea had become thoroughly established that the aecia of *Puccinia rubigo-vera* must be produced on boraginaceous species. When Plowright (1885) discovered that a rust of the *rubigo-vera* type on *Alopecurus pratensis* was connected with aecia on *Ranunculus acer*, he considered it a distinct species, naming it *Puccinia perplexans*. When he (1889) found that a similar rust on *Agropyron repens* was connected with aecia on *Thalictrum flavum*, he named it *Puccinia persistens*. Likewise, a year later he (1890) found that a rust on *Agrostis vulgaris* was connected with aecia on *Aquilegia vulgaris* and named it *Puccinia Agrostidis*.

Dietel (1892) showed by cultures that a rust on *Agropyron glaucum* was connected with aecia on *Clematis vitalba*. For this he used the name *Puccinia Agropyri* Ell. & Ev., which had just been proposed for a rust on *Agropyron glaucum* by Ellis and Everhardt (1892). The latter, however, make no comment concerning the relationship of their material.

Juel (1894) connected aecia on *Thalictrum alpinum* with uredinia and telia on *Agrostis borealis*. To this he gave the name *Puccinia borealis* Juel.

In 1894 Eriksson and Henning reported the results of extensive studies concerning the host specialization of several of the rusts of cereals and wild grasses. They point out that several rusts had been confused under the name *Puccinia rubigo-vera*. They distinguish the stripe rust of grasses under the name *Puccinia glumarum* (Schmidt) Erikss. & Henn. The rust of Hordeum species, which has a preponderant number of one-celled teliospores and which had been recognized as a variety *simplex* of *Puccinia rubigo-vera* by a number of investigators, they recognized as a species under the name *Puccinia simplex* (Körn.) Erikss. & Henn.

For the leaf rust on wheat, rye, and a number of wild grasses with scattered uredinia and telia, they proposed the name *Puccinia dispersa* Erikss. & Henn. They thus discarded the name *Puccinia rubigo-vera*. In *Puccinia dispersa* they recognized two specialized

forms, *Secalis* and *Tritici*. Eriksson (1894) continued the study in greater detail and recognized four specialized forms of *Puccinia dispersa* f. *secalis* on *Secale cereale* with aecia on *Anchusa spp.;* f. *Tritici* on *Triticum vulgare;* f. *Bromi* on *Bromus arvensis* and *B. brizaeformis* and f. *Agropyri* on *Agropyron repens*. The aecial stages of the last three races were unknown. Further studies resulted in finding that these races were closely specialized, and Eriksson (1899) reached the conclusion that they should be recognized as species. He retained the name *Puccinia dispersa* for the race on rye with aecia on Anchusa. The *Tritici* race he named *Puccinia triticina;* the *Bromi* race, *Puccinia bromina;* the *Agropyri* race, *P. agropyrina*. He also named a form on *Holcus lanatus* and *H. mollis*, *Puccinia holcina*, and a form on *Trisetum flavescens*, *Puccinia Triseti*. These names have been rather generally adopted, especially *Puccinia dispersa* for the leaf rust of rye and *Puccinia triticina* for the leaf rust of wheat, and are now used in the literature which has developed in the field of plant pathology.

The recognition of species largely on the grounds of host specialization continued. F. Müller (1900) showed that rust of the *Puccinia rubigo-vera* type on species of Bromus was connected with aecia on *Symphytum officinale* and *Pulmonaria montanum*, whereas a weak development of pycnia was obtained on *Anchusa officinalis* and *Nonnea rosea*, and negative results with *Anchusa arvensis*, *Cerinthe alpina*, *Cynoglossum officinale*, *Echium vulgare*, *E. rubrum*, *Myosotis arvensis*, *M. silvatica*, *Symphytum officinale*, *Omphalodes verna*, and *Pulmonaria officinale*. To this he gave the name *Puccinia Symphyti-Bromorum*.

Fischer proved a connection between aecia on *Actaea spicata* and rust of *Triticum* (*Agropyron*) *caninum*. To this he (1901) gave the name *Puccinia Actaeae-Agropyri* Ed. Fisch. Tranzschel (1907) demonstrated that rust on *Triticum caninum* produced aecia on *Trollius europaeus*, and gave it the name *Puccinia Dietrichiana*.

Arthur (1903) was successful in connecting a rust of the *Puccinia rubigo-vera* type on *Elymus virginicus* L. with aecia on *Impatiens aurea* Muhl. To this he gave the name *Puccinia Im-*

patientis. Klebahn has applied the name *Puccinia Impatienti-Elymi* Arth. to this. Arthur later (1909) connected aecia on *Thalictrum dioicum* and *T. sparsiflorum* with rust on *Bromus Porteri* and gave this the name *Puccinia alternans* Arth. Arthur (1909) also connected aecia on *Aquilegia canadensis* with rust on *Agropyron biflorum* and named it *Puccinia obliterata* Arth.

Mayor (1911) found that rust on *Elymus europaeus* was connected with aecia on *Actaea spicata* and gave it the name *Puccinia Actaeae-Elymi.* Arthur (1916) showed that rust on *Festuca Thuberi* connected with aecia on *Thalictrum dioicum* and named it (1919) *Puccinia Cockerelliana* Bethel.

Lüdi (1918) connected aecia on species of Aconitum with rust on *Festuca rubra commutata* and *F. rubra violacea* and gave this the name *Puccinia Aconiti-rubrae.* Fischer and Mayor (1924) found that rust on *Trisetum distichophyllum* was connected with aecia on *Thalictrum foetidum* and gave it the name *Puccinia Thalictri-distichophylli.*

There have, therefore, been an extensive subdivision and a recognition of species in *Puccinia rubigo-vera,* of which those mentioned above are only a part. However, there has been some tendency in the opposite direction. Arthur and Fromme (1920) in their treatment of the grass rusts of North America have combined under the name *Dicaeoma Clematidis* (DC.) Arth. all those rusts of the *rubigo-vera* type which they considered had aecia on species of the Ranunculaceae. The species as they conceived it has as synonyms *Puccinia Elymi* Westend., *P. triarticulata* Berk. & Curt., *P. tomipara* Trel., *P. persistens* Plowr., *P. Agrostidis* Plowr., *P. Agropyri* Ell. & Ev., *P. Aquilegiae* Lagerh., *P. Clematidis* Lagerh., *P. adspersa* Dietel & Holw., *P. triticina* Erikss., *P. agropyrina* Erikss., *P. Actaeae-Agropyri* Ed. Fisch., *P. paniculariae* Arth., *P. triticorum* Speg., *P. cinerea* Arth., *P. alternans* Arth., *P. obliterata* Arth., *P. Actaeae-Elymi* Mayor, and *P. wyomensis* Arth. They list aecia on species of Aconitum, Actaea, Anemone, Aquilegia, Cimicifuga, Clematis, Delphinium, Isopyrum, Ranunculus, and Thalictrum, and uredinia and telia on species of Aegilops, Agropyron, Alopecurus, Avena, Bromus, Elymus, Festuca, Hordeum, Hystrix, Melica, Panicularia, Poa, Puccinellia,

Scolochoa, Sitanion, Trisetum, and Triticum. They have kept separate the rust on *Anchusa officinalis* and *Secale cereale* under the name *Dicaeoma Asperifolii* (Pers.) Kuntze; rust with aecia on various species of Hydrophyllaceae and Boraginaceae and uredinia and telia on species of Agropyron, Elymus, and Sitanion under the name *Dicaeoma apocrypta;* rust with aecia on species of Impatiens and uredinia and telia on species of Agrostis, Cinna, Elymus, Hordeum, and Hystrix under the name *Dicaeoma Impatientis* (Schw.) Arth. Mains and Jackson (1926) have pointed out that these do not differ to any marked degree morphologically and suggest that they be united under the name *Puccinia rubigo-vera.*

Cunningham (1923) also has reached the conclusion that "biologic specialization alone is not considered a specific character." He recognized *Puccinia dispersa* Erikss. & Henn. and included *Puccinia dispersa* Erikss., *P. secalina* Grove, *P. bromina* Erikss., *P. Symphyti-Bromorum* F. Müller, and *P. Triseti* Erikss. as synonyms. This group of *Puccinia rubigo-vera* has boraginaceous species for aecia hosts, so far as known. To the group having ranunculaceous aecia, he applies the name *Puccinia Elymi* Westend. and includes *P. perplexans* Plowr., *P. persistens* Plowr., *P. Agrostidis* Plowr., *P. Agropyri* Ell. & Ev., *P. borealis* Juel, *P. Actaeae-Agropyri* Ed. Fisch., *P. Actaeae-Elymi* Mayor, *P. alternans* Arth., *P. obliterata* Arth., *P. agropyrina* Erikss., and *P. triticina* Erikss. as synonyms.

Cunningham, therefore, has a similar species concept to Arthur. He, however, maintains that according to the international rules of botanical nomenclature *Puccinia Elymi* Westend. should be used, since he considers it the oldest name employed for the telia stage.

Lagerheim (1898), however, has examined the type of *Puccinia Elymi* and states that Westendorp's material has three-celled teliospores; Westendorp apparently mistook the lowest cell for a pedicel. It seems very doubtful whether this rust should be considered a part of *Puccinia rubigo-vera,* unless it can be shown that the three-celled condition is an extreme, fluctuating variation. If it is a permanent stable character, it would seem best to

treat the rust as a closely related species. *Puccinia triarticulata* Berk. & Curt. probably belongs here. *Puccinia tomipara* Trel., another rust with multicellular teliospores, should also be considered a separate species.

Both *Puccinia striaeformis* Westend. and *Puccinia straminis* Fuckel have been assigned to *Puccinia rubigo-vera*. However, to judge from the descriptions which emphasized the arrangement of the sori in lines, it seems doubtful whether they apply to the rust as here considered. Both these names have had only a limited use and usually in a restricted sense. Even if it is possible by the examination of type material to show that these names apply to this rust, it seems rather doubtful whether there is anything gained by their use.

From De Candolle's (1815) description of *Uredo rubigo-vera* there seems to be no good reason for assuming that he was not dealing with the rusts of wheat and rye, which have recently been known as *Puccinia triticina* Erikss. and *P. dispersa* Erikss. & Henn. When Winter (1884) placed this in Puccinia under the name *Puccinia rubigo-vera* (DC.) Wint., he emphasized this concept, since he listed aecia on boraginaceous species as aecial hosts. As has been stated, the name *Puccinia rubigo-vera* was more or less generally used by many investigators as late as 1911, when it was superseded by the multitude of names given to divisions of the species. The fact that *Puccinia glumarum* (Schmidt) Erikss. & Henn. and *P. anomala* Rostr. (*P. simplex* (Körn.) Erikss. & Henn.) were not recognized as species for some time and that collections of these species were included in *Puccinia rubigo-vera* by many of the earlier investigators should not prevent the use of the name. If we recognize the species *Puccinia glumarum* and *P. anomala*, the name *Puccinia rubigo-vera* (DC.) Wint. applies to a very prevalent species of rust on grasses which has the general type of the leaf rust of wheat (*Puccinia triticina* of Eriksson) and which can be divided into a number of races that have been generally recognized as distinct species.

This is the concept that the writer wishes to employ in this paper. It would, therefore, seem that the name *Puccinia rubigo-vera* (DC.) Wint. is desirable from the standpoint both of the con-

cept employed and of usage. The writer can see no advantage, but rather a number of disadvantages, in earlier names, even if such can be shown to apply, since they were all used to a limited extent and for a restricted concept, and he would like to propose the establishment of the name *Puccinia rubigo-vera* for the concept here employed.

Puccinia rubigo-vera, as here used, therefore, should have as synonyms *Puccinia Aconiti-rubrae* Lüdi, *P. Actaeae-Agropyri* Ed. Fisch., *P. Actaeae-Elymi* Mayor, *P. Agropyri* Ell. & Ev., *P. Agropyri-juncei* Kleb., *P. Agropyrina* Erikss., *P. Agrostidis* Plowr., *P. alternans* Arth., *P. apocrypta* Ellis & Tracy, *P. Aquilegiae* Lagerh., *P. Asperifolii* Wetss., *P. borealis* Juel, *P. Cerinthis-Agropyrinae* Tranzsch., *P. cinerea* Arth., *P. Clematidis* Lagerh., *P. Cockerelliana* Bethel, *P. bromina* Erikss., *P. dispersa* Erikss. & Henn., *P. Dietrichiana* Tranzsch., *P. holcina* Erikss., *P. Impatientis* Arth., *P. obliterata* Arth., *P. Panicullariae* Arth., *P. perplexans* Plowr., *P. perminuta* Arth., *P. secalina* Grove, *P. subalpina* Lagerh., *P. Symphyti-Bromorum* Müller, *P. Thalictri-distichophylli* Fisch. & Mayor, *P. Triseti* Erikss., *P. triticina* Erikss., and *P. Triticorum* Speg. The description of the rust as thus conceived and the species of hosts for North America may be found by consulting *North American Flora*, Volume 7, under *Dicaeoma Asperifolii* (p. 331), *D. apocryptum* (p. 332), *D. Clematidis* (p. 333), *D. Impatientis* (p. 337), *D. Cockerellianum* (p. 329), and *D. procerum* (p. 330).

II. Methods

The methods used in this study are similar to those previously described (Jackson and Mains, 1921; Mains, 1924; Mains and Jackson, 1926). Collections of teliospores were obtained from various parts of North America and were placed outdoors in cheesecloth bags until germination occurred. In most cases this took place in the early spring after overwintering. When tests showed that the teliospores were germinable, they were placed directly upon the species to be tested under conditions favorable for the germination. In cases of successful infection pycnia usually appeared in about ten days and aecia in fifteen

days. The time, however, varied with environmental conditions. The results obtained have been designated as − when neither pycnia nor aecia were produced, 0 when pycnia were produced, and I when aecia developed.

Many aecia thus obtained were used to inoculate a series of species of grasses. In most cases several collections of seeds of a species from various sources were used. From ten to twenty seedlings of each collection were usually inoculated. Occasionally collections of aecia from natural infections in the field were used.

After such inoculations uredinia usually appeared on susceptible varieties in about seven to ten days. The results obtained from inoculating with aeciospores were usually checked by inoculating a similar series of grasses with the urediniospores thus obtained. When infection resulted in the production of only a few uredinia, the urediniospores were resown on the grasses on which they had been produced. If this resulted in increased production of uredinia, the rust was then again sown on a series of species of grasses in order to check with previous results. Often such resowings produced no increase but rather a decrease in infection.

The rather sharply defined types of reaction noted for varieties of cereals (Mains and Jackson, 1926) were not usual with the wild grasses. Occasionally highly resistant varieties showed distinct flecking, but usually this was not noticeable. Rarely, resistant species showed necrosis. It has, therefore, not been so easy to classify the relative susceptibility of some of the species of wild grasses.

In this paper the results obtained in tests of various species have been indicated as follows:

− no uredinia developed. In such cases faint flecks were sometimes noted and some necrosis was present.

t only a few, usually small, uredinia showed. They did not continue to reproduce the rust when resown.

\+ a few uredinia produced. The rusts eventually died out when resown on the species indicated.

++ moderately rusted. When the rust was resown on such species there was no increase. Occasionally there was a decrease in amount.

+++ abundantly rusted. Such species are considered the most susceptible.

III. Results

Since most of the races of *Puccinia rubigo-vera* are sharply restricted to a few species of a single genus for their aecial hosts, they will be grouped in sections according to the genera on which their aecia are produced.

A. Aecia on species of Thalictrum

a. Results obtained from inoculations from telia on grasses to aecial hosts

In these studies the following collections of telia produced aecia on species of Thalictrum:

Telia collected on *Agropyron repens* (L.) Beauv.

8818.[1] Collected on *Agropyron repens*, Nov. 2, 1918, at St. Paul, Minnesota, by H. S. Jackson. The results of inoculations are given in Table I.

23019. Collected on *Agropyron repens*, Oct. 21, 1919, at Ann Arbor, Michigan, by the writer. The results of inoculations are given in Table I.

Telia collected on species of Elymus

2918. Collected on *Elymus canadensis robustus* (S. & S.) Mack. & Beu., July 25, 1918, at Rake, Iowa, by A. C. Martin. The results of inoculations are given in Table I.

15218. Collected on *Elymus glaucus* Buckley, Nov. 20, 1918, at Corvallis, Oregon, by C. W. Hungerford. The results of inoculations are given in Table I.

16418. Collected on *Elymus virginicus* L., Jan. 21, 1919, at Madison, Wisconsin, by L. S. Cheney. *Clematis virginiana* L., *Anemone canadensis* L., and *Thalictrum dioicum* L. were inoculated. Pycnia and aecia developed only on *Thalictrum dioicum*.

16119. Collected on *Elymus glaucus*, Aug. 16, 1919, at Corvallis,

[1] The last two digits of the accession number indicate the year when the teliospores were produced. The digits to the left of these denote the serial number of the accession for the year. Thus 8818 is the 88th collection for the year 1918.

TABLE I

RESULTS OBTAINED FROM INOCULATIONS WITH SOME COLLECTIONS OF *PUCCINIA RUBIGO-VERA* PRODUCING AECIA ON SPECIES OF THALICTRUM *

SPECIES INOCULATED	SOURCE OF INOCULUM										
	Elymus sp.		Hordeum jubatum				Agropyron repens		Triticum vulgare		
	2918†	15218	3118	6918	9418	27119	8818	23019	Summary ‡ to 1921	2520	4220
Aconitum Napellus	..	–	..	..	–	..	..	..	–	..	..
Actaea alba	–	..	–	..	..	..	–	..	..	..	..
rubra	..	..	–	..	..	..	..	..	..	..	..
spicata	..	..	–	..	..	..	–	..	–	..	..
Anemone canadensis	–	–	–	..	–	..	..	..	–	–	–
cylindrica	..	..	–	–	..	..	..	..	–	–	..
Aquilegia alpina	..	–	..	..	–	..	–	..	–	..	..
canadensis	..	..	–	–	–	..	–	..	–	–	..
chrysantha	..	–	..	..	–	..	–	..	–	..	–
coerulea	–	–	–	..	–	..	–	..	..	..	..
Skinneri	..	–	..	..	..	..	..	..	–	..	..
vulgaris	..	–	..	..	–	..	–	..	–	–	..
Cimicifuga racemosa	..	–	..	..	..	..	..	..	–	..	–
Clematis Fremontii	..	–	–	..	..	..	..	..	–	–	..
ligusticifolia	–	–	–	–	..	..	..	..	–	–	–
orientalis	–	–	..	..	–	..	–	..	–	–	–
virginiana	–	–	–	–	..	..	–	..	–	–	..
Delphinium Geyeri	..	–	–	..	..	..	..	..	–	..	..
Echium vulgare	..	–	..	..	..	..	–	..	–	..	..
Hydrophyllum appendiculatum	..	–	..	..	..	..	–	..	–	–	–
Impatiens biflora	–	..	–	–	..	..	–	..	–	..	..
Mertensia virginica	..	–	..	..	..	..	..	..	–	..	..
Phacelia tanacetifolia	..	–	..	..	..	..	–	..	–	..	..
Ranunculus aconitifolius	..	–	..	..	..	..	..	..	–	..	..
Thalictrum angustifolium	..	–	..	..	..	–	0	–	– 0 §	0	–
aquilegifolium	..	0I	0I	0I	0	..	..	0	– 0 §	0	–
dasycarpum	0I	0I	0I	..	0I	0I	–	–	– 0	–	–
dioicum	..	0I	0I	0I	..	0I	–	–	– 0 §	–	–0
Fendleri	..	..	..	0I	..	..	..	..	..	–	..
paniculatum	..	..	..	..	..	0I	..	–	..	–	–
Delavayi	..	..	..	..	..	..	..	0I	0I	0I	0I
flavum	..	..	..	..	..	..	..	0I	0I	0I	0I
minus	..	..	..	..	..	–	0I	0I	– 0 §	0I	–
minus adiantifolium	..	..	..	..	..	–	..	..	– 0 §	..	..
polygamum	..	–	..	..	..	0	–	–	– 0	–	0
Trollius europaeus	..	..	..	..	–	..	..	..	–	..	..

* For other results see text.

† Accession number of collection. For data see text.

‡ Results obtained by Jackson and Mains. *Journ. Agric. Res.*, 22 (1921): 157.

§ A few aecia were occasionally produced.

Oregon, by C. E. Owens. *Hydrophyllum virginianum* L., *Clematis ligusticifolia* Nutt., and *Thalictrum sp.* were inoculated. Pycnia and aecia developed only on *Thalictrum sp.*

16719. Telia developed in the greenhouse at Lafayette, Indiana, on *Elymus canadensis* L., from the culture obtained from aecia produced on *Thalictrum dasycarpum* Fisch. & Lall., from collection 9418. A species of Thalictrum was inoculated, producing pycnia and aecia.

26019. Collected on *Elymus canadensis*, Nov. 11, 1919, at Lafayette, Indiana, by the writer. *Thalictrum dasycarpum* was inoculated and pycnia and aecia were produced.

26519. Collected on *Elymus glaucus*, Nov. 9, 1919, at Corvallis, Oregon, by C. E. Owens. *Thalictrum sp.* inoculated, producing pycnia and aecia.

Telia collected on *Hordeum jubatum* L.

2518. Collected on *Hordeum jubatum*, July 23, 1918, at Thompson, Iowa, by A. C. Martin. *Thalictrum dasycarpum* and *T. dioicum* were inoculated, both producing pycnia and aecia.

2618. Collected on *Hordeum jubatum*, July 24, 1918, at Thompson, Iowa, by A. C. Martin. *Thalictrum aquilegifolium* L. was inoculated, producing pycnia and aecia.

3018. Collected on *Hordeum jubatum*, July 25, 1918, at Rake, Iowa, by A. C. Martin. *Impatiens biflora* Walt. and *Thalictrum aquilegifolium* were inoculated. Pycnia and aecia were produced on *Thalictrum aquilegifolium.*

3118. Collected on *Hordeum jubatum*, July 26, 1918, at Madison, Wisconsin, by E. H. Toole. The results of inoculations are given in Table I.

3718. Collected on *Hordeum jubatum*, Aug. 9, 1918, by J. G. Dickson. This was sown on *Thalictrum angustifolium* L., *T. minus* L., *T. dasycarpum*, and *T. aquilegifolium.* Pycnia and aecia were produced only on *T. dasycarpum* and *T. aquilegifolium.*

6918. Collected on *Hordeum jubatum*, Sept. 23, 1918, at Britt, Iowa, by E. H. Toole. The results of inoculations are given in Table I.

7618. Telia developed on *Hordeum jubatum* in the greenhouse at Lafayette, Indiana, from a culture derived from uredinia of collection 3118. When cultured, pycnia and aecia were obtained on *Thalictrum dioicum*. Negative results were obtained with *Anemone cylindrica* Gray, *Clematis virginiana*, *Impatiens biflora*, and *Thalictrum aquilegifolium*.

7718. Telia developed on *Hordeum jubatum* in the greenhouse at Lafayette, Indiana, from a culture derived from uredinia collected by E. H. Toole, July 26, 1918, at Madison, Wisconsin. When cultured, this produced pycnia and aecia on *Thalictrum dasycarpum*. Negative results were obtained with *Anemone cylindrica*, *Clematis virginiana*, and *Thalictrum aquilegifolium*.

8218. Collected on *Hordeum jubatum*, Nov. 1, 1918, at Madison, Wisconsin, by H. S. Jackson. *Thalictrum angustifolium* and *T. dioicum* were inoculated. Pycnia and aecia developed only on *T. dioicum*.

9418. Collected on *Hordeum jubatum*, Nov. 4, 1918, at Fargo, North Dakota, by H. S. Jackson. The results of inoculations are given in Table I.

9518. Collected on *Hordeum jubatum*, Nov. 4, 1918, at Fargo, North Dakota, by H. S. Jackson. *Thalictrum aquilegifolium* and *T. dasycarpum* were inoculated, producing pycnia and aecia.

10618. Collected on *Hordeum jubatum*, Nov. 1918, at Madison, Wisconsin, by J. G. Dickson. *Impatiens biflora* and *Thalictrum dioicum* were inoculated. Pycnia and aecia were produced on *Thalictrum dioicum*.

16619. Telia developed in the greenhouse on *Hordeum jubatum* at Lafayette, Indiana, from the culture obtained from aecia produced on *Thalictrum dasycarpum* from collection 9418. *Thalictrum dasycarpum* was inoculated, producing pycnia and aecia.

18119. Telia developed in the greenhouse at Lafayette, Indiana, on *Hordeum jubatum* from the culture obtained from aecia produced on *Thalictrum dasycarpum* from collection 7718. *Thalictrum dasycarpum* was inoculated, producing pycnia and aecia.

22119. Collected on *Hordeum jubatum*, Oct. 11, 1919, at Charleston, Illinois, by L. S. Cheney. *Thalictrum dasycarpum* was inoculated, producing pycnia and aecia.

24719. Collected on *Hordeum jubatum*, Oct. 20, 1919, at Madison, Wisconsin, by E. H. Toole. *Anemone cylindrica*, *Clematis virginiana*, and *Thalictrum dioicum* were inoculated. Pycnia and aecia were produced on *T. dioicum* only.

26319. Collected on *Hordeum jubatum*, Nov. 11, 1919, at Lafayette, Indiana, by the writer. This, when cultured, produced pycnia and aecia on *Thalictrum dasycarpum*, *T. paniculatum* Bess., and *T. polygamum* Muhl. Negative results were obtained with *T. angustifolium*, *T. dipterocarpum* Franchet, and *T. minus adiantifolium* Bess.

27119. Collected on *Hordeum jubatum*, Nov. 17, 1919, at Rock Island, Illinois, by L. S. Cheney. The results of inoculations are given in Table I.

Telia collected on *Triticum vulgare* Vill.

The results of studies in 1919 and 1920, in which the aecial stage of the leaf rust of wheat was discovered, have been previously reported. (Jackson and Mains, 1921.) These have been summarized in Table I under the heading "Summary to 1921." In 1921 additional collections were studied as follows:

2220. Collected on wheat, May 27, 1920, at Athens, Georgia, by R. R. Childs. When cultured, this produced pycnia and aecia on *Thalictrum flavum* L. and *T. Delavayi* Franchet. Pycnia were produced on *Thalictrum nutans* Gilib. Negative results were obtained with *Anemonella thalictroides* (L.) Spach., *Thalictrum angustifolium*, *T. aquilegifolium*, *T. dasycarpum*, *T. elegans* Wall., *T. Fendleri* Engelm., *T. minus*, *T. paniculatum*, and *T. polygamum*.

2320. Collected on wheat, May 26, 1920, at Clemson College, South Carolina, by C. A. Ludwig. This produced pycnia and aecia on *Thalictrum flavum*. Pycnia occurred on *Thalictrum elegans*. Negative results were obtained with *Anchusa officinalis* L., *Anemonella thalictroides*, *Clematis flammula* L., *C. Gouriana* Roxb., *C. grata* Wall., *C. montana* Buch.-Ham., *C. ochroleuca* Ait., *Thalictrum angustifolium*, *T. aquilegifolium*, *T. cultratum* Wall., *T. dioicum*, *T. dipterocarpum*, *T. nutans*, *T. paniculatum*, *T. polygamum*, *T. saxatile* Schleich., and *T. simplex* L.

2520. Collected on wheat, June 12, 1920, at Clemson College, South Carolina, by C. A. Ludwig. The results obtained on the species used for rusts from wild grasses are shown for comparison in Table I. In addition to *Thalictrum Delavayi, T. flavum* and *T. minus,* this rust produced pycnia and aecia on *Anemonella thalictroides* and *Thalictrum saxatile.* In addition to those shown in Table I, negative results were obtained with *Aquilegia eximia* Borbas, *Cerinthe minor* L., *Clematis Davidiana* Decne, *C. flammula, C. Gouriana, C. grata, C. integrifolia* L., *C. lasiantha* Nutt., *C. montana, C. ochroleuca, C. paniculata* Thunb., *C. recta* L., *Cynoglossum officinale* L., *Hydrophyllum virginianum* L., *Isopyrum biternatum* (Raf.) T. & G., *Phacelia californica* Cham., *P. distans* Benth., *Thalictrum cultratum, T. dipterocarpum, T. elegans, T. nutans, T. occidentale* Gray, and *T. simplex.* The results obtained with *Anemonella thalictroides* are of interest, since this is the only case in which aecia of the leaf rust of wheat have been produced outside the genus Thalictrum.

2820. Collected on wheat, June 12, 1920, at Clemson College, South Carolina, by C. A. Ludwig. This produced pycnia and aecia on *Thalictrum flavum, T. Delavayi,* and *T. minus;* pycnia and a few aecia on *T. dioicum* and *T. elegans;* pycnia only on *T. glaucum* Desf., *T. Fendleri, T. nutans,* and *T. polygamum.* Negative results were obtained with *Anemonella thalictroides, Thalictrum angustifolium, T. aquilegifolium, T. dipterocarpum, T. paniculatum,* and *T. simplex.* It is interesting to contrast the results obtained from this collection with those obtained from the previous collection from the same locality. The differences suggest that there may be forms of the leaf rust of wheat which may be separated by aecial hosts.

2920. Collected on wheat, June 10, 1920, at Knoxville, Tennessee, by Carl Kurtzweil. This produced pycnia and aecia on *Thalictrum flavum.* Negative results were obtained with *Thalictrum dipterocarpum.*

3120. Collected on wheat, June 15, 1920, at Raleigh, North Carolina, by F. A. Wolf. Pycnia and aecia were produced on *Thalictrum flavum* and *T. Delavayi* and a few pycnia on *T. cultratum.* Negative results were obtained with *T. angustifolium, T.*

aquilegifolium, T. dasycarpum, T. dioicum, T. elegans, T. minus, T. nutans, T. occidentale, T. paniculatum, T. polygamum, T. saxatile, and *T. simplex.*

4220. Collected on wheat, June 22, 1920, at Arlington, Virginia, by the writer. In addition to the results given in Table I, pycnia were produced on *Thalictrum saxatile* and negative results were obtained on *Anchusa officinalis, Anemone vitifolia* Buch.-Ham., *Anemonella thalictroides, Aquilegia pyrenaica* DC., *Clematis Davidiana, C. grata, C. integrifolia, C. montana, C. paniculata, Hydrophyllum virginianum, Myosotis scorpoides* L., *Ranunculus acris* L., *Thalictrum cultratum, T. dipterocarpum, T. elegans, T. nutans,* and *T. simplex.*

4720. Collected on wheat, June 31, 1920, at Hummelstown, Pennsylvania, by G. N. Hoffer. This produced pycnia and aecia on *Thalictrum flavum.*

5020. Collected on wheat, July 10, 1920, at Lafayette, Indiana, by the writer. This produced pycnia and aecia on *Thalictrum Delavayi* and a few pycnia on *T. dipterocarpum.*

7320. Collected on wheat, July 10, 1920, at Tifton, Georgia, by R. R. Childs. This produced pycnia and aecia on *Thalictrum flavum* and *T. Delavayi.* Negative results were obtained with *Aquilegia pyrenaica, Clematis grata, C. integrifolia, C. montana, Ranunculus acris* L., *Thalictrum angustifolium, T. aquilegifolium, T. dasycarpum, T. dioicum, T. dipterocarpum, T. elegans, T. minus, T. nutans, T. paniculatum, T. polygamum, T. saxatile,* and *T. simplex.*

During the winter of 1927–28 at Lafayette, Indiana, plants of *Thalictrum aquilegifolium, T. angustifolium, T. Fendleri, T. flavum, T. glaucum, T. minus,* and *T. polygamum* were mulched with wheat straw bearing telia of the leaf rust of wheat. On May 24, 1928, pycnia and aecia were first observed on *Thalictrum flavum* and *T. glaucum.* The infection did not become abundant in either case. It is interesting to note that leaf rust had developed to a considerable extent from overwintered uredinial mycelium in the wheat fields of the vicinity before aecia had appeared on Thalictrum.

The results obtained in these studies show that *Puccinia rubigo-*

vera contains a group of races apparently restricted to species of Thalictrum for their aecial hosts. The development of aecia on *Anemonella thalictroides*, as well as on Thalictrum by one collection from wheat, is the only exception. This group may be still further subdivided according to the species of Thalictrum which serve as hosts. Thus a group of races from species of Elymus and *Hordeum jubatum* develop aecia on *Thalictrum aquilegifolium*, *T. dasycarpum*, *T. dioicum*, and probably *T. Fendleri* and *T. paniculatum*. These species are not favorable hosts for another group of races from *Agropyron repens* and wheat, *Triticum vulgare*, which produce aecia on *Thalictrum Delavayi* and *T. flavum*, and somewhat irregularly on *T. minus*. It is interesting to note in this connection that the races on the introduced species *Agropyron repens* and *Triticum vulgare* have foreign species of Thalictrum for aecial hosts and that native North American species are apparently much less favorable hosts. These races, after having been introduced, are apparently able to survive without the aecial stage, continuing from one season to the next in the uredinial stage through mycelium overwintering in the tissue of the host. The negative results with *Thalictrum angustifolium* and *T. polygamum* may be indicative of other races, since both of these have been listed as aecial hosts. The latter, however, was hardly used extensively enough to enable one to draw conclusions.

b. Results obtained by inoculations from aecia on Thalictrum to various species of grasses

In many cases the aecia produced on species of Thalictrum were used to inoculate a series of grasses for the purpose of studying the host specialization throughout the life cycle. In some cases aecia collected in the field were employed. A few cultures were made from uredinia directly associated with the telia from which aecia were produced on Thalictrum. Not all of the species of grasses were available for each of the cultures of rust and consequently complete data for all of them were not obtained.

Cultures from the following sources were used, with the results given in Tables II and III (pp. 308, 309):

Ag 10.[2] Collected on *Agropyron repens*, Nov. 2, 1918, at St. Paul, Minnesota, by H. S. Jackson. The uredinia used for this culture were associated with collection 8818 of telia, which produced aecia on *Thalictrum minus*.

Ag 30. Collected on *Agropyron repens*, July 10, 1919, at Madison, Wisconsin, by the writer. This was not connected with aecia, but is included on account of similarity to Ag 10.

El 11. Collected on *Elymus glaucus*, Nov. 1918, at Corvallis, Oregon, by C. W. Hungerford. To judge from field associations this rust was apparently connected with aecia on Thalictrum.

El 52. From *Elymus canadensis*, Nov. 11, 1919, at Lafayette, Indiana, collected by the writer. This culture was from uredinia associated with collection 26019 of telia from which aecia on *Thalictrum dasycarpum* were obtained.

Th 4. From aecia on *Thalictrum dasycarpum* obtained by inoculating with collection 9418 from *Hordeum jubatum*.

Th 5. From aecia on *Thalictrum dasycarpum* obtained by inoculating with collection 2918 from *Elymus sp.*

Th 9. From aecia on *Thalictrum dasycarpum* obtained by inoculating with collection 9518 from *Hordeum jubatum*.

Th 12. From aecia on *Thalictrum dasycarpum* obtained by inoculating with collection 7718 from *Hordeum jubatum*.

Th 13. From aecia on *Thalictrum dioicum* obtained by inoculating with collection 8218 from *Hordeum jubatum*.

Th 15. From aecia on *Thalictrum dioicum* obtained by inoculating with collection 10618 from *Hordeum jubatum*.

Th 16. From aecia on *Thalictrum dioicum* developed by inoculating with collection 7618 from *Hordeum jubatum*.

Th 17. From aecia on *Thalictrum aquilegifolium* developed by inoculating with collection 3018 from *Hordeum jubatum*.

Th 24. From aecia on *Thalictrum Fendleri* collected June 28, 1919, at Hot Springs, Colorado, by E. Bethel.

Th 32. From aecia on *Thalictrum dasycarpum* developed by inoculating with collection 22119 from *Hordeum jubatum*.

[2] The accession numbers of cultures from aecia or uredinia indicate the genus of the host plant and the serial number of the collection. Thus Ag 10 was the tenth collection from Agropyron, El 11 the eleventh from Elymus, and Th 4 the fourth from Thalictrum.

Th 33. From aecia on *Thalictrum dasycarpum* developed by inoculating with collection 27119 from *Hordeum jubatum.*

Th 48. From aecia on *Thalictrum sp.* developed by inoculating with collection 2619 from *Hordeum jubatum.*

Th 81. From aecia on *Thalictrum sp.* collected June 29, 1921, at Pagosa Springs, Colorado, by E. Bethel.

The last column in Table III, "race *Tritici*," gives the results previously reported (Jackson and Mains, 1921). This summarizes three cultures from aecia on *Thalictrum flavum* and on *T. Delavayi*, which had been produced in the greenhouse from inoculations with telia from wheat.

c. Results obtained by inoculations from uredinia on wheat to various species of grasses

In addition to the collections of the rust of wheat derived from aecia on Thalictrum a considerable number of collections of uredinia on wheat obtained from various parts of the United States were studied on the wild grasses, and especially on more than twelve hundred varieties, strains, and selections of the various species of wheat. Part of these studies dealing with varieties of wheat have been reported (Mains and Jackson, 1926), in which it has been shown that certain of the agronomic varieties differ in their reaction to various physiologic forms of the rust which they serve to differentiate. (See also Scheibe, 1928.)

It is not possible here to give the details of these investigations. Summarized, the results obtained are as follows: *Triticum compactum* as a whole was found to be very susceptible; only one or two strains of those studied showed any signs of resistance. *Triticum vulgare* is for the most part susceptible in the seedling stage. A number of strains of this species showed resistance to some of the physiologic forms of the rust, frequently to a very marked degree. Most of these were, however, susceptible to other physiologic forms of the rust. Only a few have shown promise of being resistant to the race *Tritici* as a whole. Fewer strains of *Triticum spelta* L. were investigated, but this species apparently is similar to the preceding one in its susceptibility. Only a few strains of *Triticum turgidum* L. and *T. polonicum* L. were studied. Most

TABLE II

REACTION OF SPECIES OF GRASSES TO COLLECTIONS OF RACES *VULGARIS* AND *ANOMALA* OF *PUCCINIA RUBIGO-VERA* DERIVED FROM AECIA ON THALICTRUM

SPECIES INOCULATED	RACE VULGARIS								RACE ANOMALA
	Th 4*	Th 5	Th 13	Th 15	Th 16	Th 17	Th 32	Th 48	Th 12
Agropyron caninum	..	t	−	−	−	−	..	−	−
cristatum	..	..	..	−	−	−	..	..	..
desertorum	..	..	..	..	−	−	..	..	..
intermedium	..	−	−	−	−	..	..	..	..
pseudorepens	t	..	−	t	−	t	..	..	..
repens	..	−	−	−	−	−	..	−	−
Smithii	−	−	−	−	−	t	..	..	t
tenerum	..	−	−	−	−	−	−	−	−
Alopecurus pratensis	−	−	..	..	−	..	..	..	−
Bromus altissimus	..	−	..	..	−	..	..	..	..
carinatus	−	−	..	−	−	−	..	..	−
ciliatus	−	−	..	−	−	−	−	−	−
erectus	..	..	..	..	−	..	..	..	..
hordeaceus	−	..	−	..	−	..	..	..	..
inermis	..	..	−	..	..	..	..	..	..
japonicus	..	−	−	..	−	−	..	..	−
Kalmii	..	−	−	..	−	−	..	..	..
polyanthus	−	..	−	−	−	−	..	..	−
secalinus	..	..	−	..	−	−	..	..	−
sitchensis	−	−	−	−	−	−	..	..	..
sterilis	..	−	−	..	−	−	..	..	..
tectorum	..	..	−	..	−	−	..	..	−
villosus	..	..	..	..	..	−	..	..	..
vulgaris	..	..	..	..	−	−	..	..	..
Elymus arkansanus	..	−	−	..	−	..	..	..	..
australis	+	+	t	+	−	t	..	..	t
canadensis	+++	+++	+++	+++	+++	++	+++	+++	t
condensatus	−	+	t	..	+	t	..	..	t
glaucus	+	++	+	t	t	−	..	..	t
robustus	..	..	..	..	++	..	..	..	+
virginicus	+	+	t	+	t	+	..	+	+++†
Hordeum Gussoneanum	..	t	−	t	..	t	..	..	..
jubatum	+++	+++	+++	+++‡	+++	+++	+++	+++	+++
murinum	−	−	−	−	−	t	−	−	−
nodosum	+	t	t	+	t	t	..	..	++
pusillum	+	+	t	+	t	+	..	..	+
vulgare §	−	−	−	t	−	..	..	..	−
Hystrix Hystrix	+	t	t	t	t	−	..	..	+
Secale cereale ‖	..	−	−	−	−	−	..	..	−
Sitanion Hystrix	+	t	+	+	+	+	++	..	+
Triticum vulgare ¶	−	..	−	t	−	−	−	..	−
Trisetum spicatum	−	..	−	−	−	−	..	..	−

* For explanation of collection numbers see text.

† One collection of *Elymus virginicus* was somewhat resistant.

‡ One collection of *Hordeum jubatum* was somewhat resistant. It was susceptible to all other collections of the race.

§ The variety Oderbrucker was used.

‖ The variety Virginia was used.

¶ The varieties Dawson Golden Chaff and Red Wave were used.

TABLE III

REACTION OF SPECIES OF GRASSES TO COLLECTIONS OF RACES *CIRCUMSCRIPTA*, *HORDEICOLA*, *ELYMICOLA*, *OCCIDENTALIS*, *ALTERNANS*, *PERSISTENS*, AND *TRITICI*, DERIVED FROM AECIA ON THALICTRUM

SPECIES INOCULATED	Race circumscripta		Race hordeicola	Race elymicola	Race occidentalis	Race alternans	Race persistens		Race Tritici
	Th 9*	Th 33	Th 24	El 52	El 11	Th 81	Ag 10	Ag 30	Summary
Agropyron caninum	..	−	−	t	−	−	−	t	−
cristatum	..	..	..	..	..	..	−	..	−
desertorum	..	..	..	..	−	..	−	..	−
intermedium	..	..	..	..	−	..	−	−	..
pseudorepens	−	..	..	..	−	..	+	++	−
repens	..	−	−	..	−	−	+++	+++	−
Smithii	−	..	−	t	−	..	−	−	..
tenerum	..	−	−	t	−	−	t	−	−
Bromus carinatus	..	−	..	..	−	+++	..	−	..
ciliatus	−	..	..	..	..	−	..	..	..
erectus	..	..	..	..	..	−	..	..	..
hordeaceus	..	..	..	..	..	t	..	..	..
inermis	..	..	..	..	..	−	..	..	..
japonicus	..	..	..	..	−	−	−	..	..
polyanthus	..	..	..	..	−	..	..	..	..
Pumpellianus	..	..	..	..	..	+++	..	..	..
purgans	..	..	..	..	..	−	..	..	..
Richardsonii	..	..	..	..	..	+++	..	..	..
secalinus	..	..	..	..	..	−	..	..	..
sitchensis	..	..	..	..	−	+++	..	..	..
sterilis	..	..	..	..	..	+	..	..	..
tectorum	..	..	..	..	..	t	−	..	..
vulgaris	..	..	..	..	..	−	..	..	..
Elymus australis	..	..	−	..	−	..	..	..	−
canadensis	+	−	+	+++	+++	−	−	−	−
condensatus	t	..	..	−	+++	..	..	..	..
glaucus	..	+	..	+++	+++	−	..	..	−
robustus	t	..	−	+++	+++	..	−	..	..
striatus	..	..	..	+++	..	..	..	..	..
triticoides	..	..	..	−	..	..	..	..	..
virginicus	t	−	−	+++	−	−	..	−	−
Hordeum Gussoneanum	−	..	−	+++	..	..	..	..	−
jubatum	+++	+++	+++	−	+++†	−	−	−	−
murinum	−	−	−	−	−	..	..	..	−
nodosum	t	+	+++	..	−	..	..	..	..
pusillum	−	..	t	..	++	..	−	−	−
vulgare ‡	..	−	−	−	−	..	−	..	−
Hystrix Hystrix	−	−	−	+++	−	..	−	−	−
Secale cereale §	−	−	−	−	−	−	−	..	t
Sitanion Hystrix	−	+	−	−	..	..	..	..	−
jubatum	..	..	..	−	..	..	..	..	..
Triticum vulgare ‖	−	−	−	−	−	−	−	−	+++

* For explanation of collection numbers see text.
† One collection of *Hordeum jubatum* was somewhat resistant.
‡ The variety Charlottestown No. 80 was used.
§ The variety Virginia was used.
‖ The varieties Dawson Golden Chaff and Red Wave were used.

of these varied in their reaction to various physiologic forms of the race, being susceptible to some of the forms and resistant to others. Most of the strains of *Triticum durum* Desf. showed some signs of resistance in the seedling stage; a few were moderately susceptible and a few rather resistant. This species was for the most part highly resistant in the field. Most of the strains of *Triticum dicoccum* Schrank. were resistant; a few were moderately susceptible to some physiologic forms of the race. The few strains of *Triticum monococcum* L. studied were very resistant. The two strains of *Triticum dicoccoides* Kcke. were susceptible to two physiologic forms and resistant to a third. Both strains of *Triticum aegilopoides* were resistant to three physiologic forms (p. f. 3, 5, 9).

Five species of Aegilops were observed for reaction to three physiologic forms (p. f. 3, 5, 9) of the race *Tritici* (Table IV). Both varieties of *Aegilops crassa* and one variety (*brunnea*) of *Aegilops squarrosa* were susceptible. One strain of *A. squarrosa* (814) was resistant. One variety (*rubiginosa*) of *A. cylindrica* was susceptible to two physiologic forms and resistant to the third, and three strains were more or less resistant to all three forms. One strain of *A. ovata* was more or less susceptible, whereas the other was highly resistant. All the strains of *Aegilops triuncialis* were more or less resistant.

Seventy varieties and strains of rye, *Secale cereale,* were studied. No stable differences were noted between these; all varieties were very resistant. Often only faint flecking was produced. Occasionally small uredinia accompanied the flecks.

Arthur and Fromme (1920) list under *Dicaeoma Clematidis* a collection of rust on *Hordeum vulgare* L. from Texas. An examination of this material (Barth., N. Am. Ured. 263, Fungi Columb. 3465) shows abundant two-celled teliospores, indicating that the collection may belong in this species. To throw more light on the question whether barley is a host for the leaf rust of wheat, 195 strains and varieties of barley (*Hordeum vulgare, H. distichon* L., *H. defeciens* Steud., and *H. intermedium*) were inoculated with physiologic form 9. Forty-eight varieties developed no visible signs of infection; 139 showed flecks. Only 8 varieties, Bohemian C.I. 204, Nepal C.I. 247, Nepal C.I. 250, Club Mariout C.I. 261,

Kinver Chevalier C.I. 587, Hannchen C.I. 602, Peru C.I. 653, and an unnamed C.I. 1383, developed uredinia. On these, the uredinia were small and usually accompanied by more or less chlorosis. Though these results do not exclude the possibility that

TABLE IV

REACTION OF SPECIES OF AEGILOPS TO PHYSIOLOGIC FORMS 3, 5, AND 9 OF *PUCCINIA RUBIGO-VERA TRITICI*

AEGILOPS SPECIES	ACC. NO.	REACTION TO PHYSIOLOGIC FORMS *		
		p. f. 3	p. f. 5	p. f. 9
Aegilops cylindrica	804	1-2	2-3	0
	813	0	0	0
cylindrica pubescens	812	0	0	0
cylindrica rubiginosa	808	3-4	1	4
crassa	805	4	3-4	4
	806	4	3-4	4
ovata	803	3	3-4	2+
	811	0	0-1	0
squarrosa	814	1-2	1-2	0-1
squarrosa brunnea	807	3-4	3-4	3-4
triuncialis	815	0-2	0-2	0
	W	0-1	2	0
	809	0-2	2-3	0-2
triuncialis nigro-albescens	810	0	0	1-2

* Designations of reactions are as follows: 0, highly resistant, no uredinia, infection indicated by small necrotic areas or flecks; 1, very resistant, uredinia small, accompanied by necrosis, many necrotic areas without uredinia; 2, moderately resistant, uredinia of moderate size, accompanied by necrosis, necrotic areas occasionally without uredinia; 3, moderately susceptible, uredinia of moderate size, accompanied by more or less chlorosis; 4, very susceptible, uredinia well developed, little or no chlorosis.

there may be some varieties of barley which are susceptible to some of the physiologic forms of the race *Tritici*, they indicate that barley is not usually a favorable host. Observations in the field would also support this conclusion, since uninfected barley is frequently found in close proximity to heavily rusted wheat.

A number of inoculations with various collections of the leaf

rust of wheat on species of wild grasses did not result in finding any favorable hosts. *Hordeum pusillum* Nutt. and *H. nodosum* L. often developed a few small uredinia. *Agropyron repens, A. tenerum* Vasey, *Elymus canadensis, E. virginicus,* and *Hordeum jubatum* occasionally produced a few uredinia. On the following species there was no sign of infection, or else infection was only occasionally evident as flecks: *Agropyron caninum* (L.) Beauv., *A. desertorum* Schult., *A. Smithii* Rydb., *Agrostis alba* L., *Agrostis stolonifera* L., *Agrostis perennans* (Walt.) Tuckerm., *Agrostis verticillata* Vill., *Anthoxanthum odoratum* L., *Arrhenatherum elatius* (L.) Beauv., *Bromus altissimus* Pursh., *B. brizaeformis* Fisch. & Mey., *B. carinatus* Hook. & Arn., *B. ciliatus* L., *B. erectus* Huds., *B. hordeaceus* L., *B. inermis* Leyss., *B. japonicus* Thunb., *B. Kalmii* Gray, *B. mollis* L., *B. polyanthus* Scribn., *B. pumpellianus* Scribn., *B. Richardsonii* Link, *B. rubens* L., *B. sitchensis* Bongard., *B. sterilis* L., *B. tectorum* L., *B. villosus* Gmel., *Elymus arkansanus* Scribn. & Ball, *E. australis* Scribn. & Ball, *E. condensatus* Presl., *E. glaucus, E. striatus* Willd., *Festuca elatior* L., *F. rubra* L., *F. ovina* L., *F. dumetorum* Phil., *F. tenuifolia* Sibth., *F. megulura* Nutt., *Hordeum Gussoneanum* Parl., *H. murinum* L., *Hystrix Hystrix* Millsp., *Lolium multiflorum* Lam., *L. temulentum* L., *Secale montanum* Guss., and *Sitanion Hystrix* (Nutt.) J. C. Smith.

d. Summary of races of Puccinia rubigo-vera with aecia on species of Thalictrum

It is evident from Tables II and III not only that *Puccinia rubigo-vera* may be divided into groups according to the species of Thalictrum which serve for aecial hosts, but that these may be subdivided according to the species of grasses to which such subgroups are specialized. On this basis the following races, formae speciales, have been recognized:

1. Puccinia rubigo-vera vulgaris, nov. sp. f.

Aecial hosts. — This race of *Puccinia rubigo-vera* produces aecia on *Thalictrum dasycarpum* and *Thalictrum dioicum. Thalictrum aquilegifolium* is apparently somewhat less favorable.

Thalictrum paniculatum and *Thalictrum polygamum* are probably also more or less favorable hosts, according to the results obtained with one collection (26319).

Negative results were obtained with *Aconitum Napellus, Actaea alba, A. rubra, A. spicata, Anemone canadensis, A. cylindrica, Aquilegia alpina, Aq. canadensis, Aq. chrysantha, Aq. coerulea, Aq. vulgaris, Clematis Fremontii, C. ligusticifolia, C. orientalis, C. virginiana, Delphinium Geyeri, Impatiens biflora, Thalictrum angustifolium, T. dipterocarpum, T. minus adiantifolium,* and *Trollius europaeus.*

Grass hosts. — *Elymus canadensis* and *Hordeum jubatum* are the favorable grass hosts. *Elymus robustus* probably is a susceptible species. It was not studied sufficiently, however, to enable one to draw conclusions.

Negative results or only a few, small uredinia were obtained with *Agropyron caninum, A. cristatum, A. desertorum, A. intermedium, A. pseudorepens, A. repens, A. Smithii, A. tenerum, Alopecurus pratensis, Bromus altissimus, B. carinatus, B. ciliatus, B. erectus, B. hordeaceus, B. inermis, B. japonicus, B. Kalmii, B. polyanthus, B. secalinus, B. sitchensis, B. sterilis, B. tectorum, B. villosus, B. vulgaris, Elymus arkansanus, E. australis, E. condensatus, E. glaucus, E. virginicus, Hordeum Gussoneanum, H. murinum, H. nodosum, H. pusillum, H. vulgare, Hystrix Hystrix, Secale cereale, Sitanion Hystrix, Triticum vulgare,* and *Trisetum spicatum.* A number of the species of Elymus, Hordeum, Hystrix, and Sitanion had some infection, as shown in Table II. The rust was not able to maintain itself on such hosts, and they are placed here with the more highly resistant species in which few or no signs of infection were noticed. These conclusions are based on the detailed results previously described for collections Th 4–9418, Th 5–2918, Th 13–8218, Th 15–10618, Th 16–7618–3118, Th 32–22119, and Th 48–26319.

This race is apparently prevalent on *Hordeum jubatum,* since all of the collections, except one on *Elymus canadensis robustus,* were made on *H. jubatum.* They were obtained from North Dakota, Wisconsin, Iowa, Illinois, and Indiana. This race is closely related to the races *anomala* and *Fraseri.*

2. **Puccinia rubigo-vera anomala,** nov. sp. f.

Aecial hosts. — Only one collection of this race was studied, Th 12–7718. It produced aecia on *Thalictrum dasycarpum.* Negative results were obtained with *Anemone cylindrica, Clematis virginiana,* and *Thalictrum aquilegifolium.* To judge from its apparently close relationship with the race *vulgaris,* it also will probably infect *Thalictrum dioicum* and possibly *T. paniculatum* and *T. polygamum.*

Grass hosts. — *Elymus virginicus* and *Hordeum jubatum* are the favorable grass hosts. *Hordeum nodosum* was moderately infected.

Little or no infection occurred on *Agropyron caninum, A. pseudorepens, A. repens, A. Smithii, A. tenerum, Alopecurus pratensis, Bromus carinatus, B. ciliatus, B. japonicus, B. polyanthus, B. secalinus, B. tectorum, Elymus australis, E. canadensis, E. condensatus, E. glaucus, E. robustus, Hordeum murinum, H. pusillum, H. vulgare, Hystrix Hystrix, Secale cereale, Sitanion Hystrix, Triticum vulgare,* and *Trisetum spicatum.*

This race is mostly differentiated from *vulgaris* by the resistance of *Elymus canadensis* and the susceptibility of *E. virginicus.*

3. **Puccinia rubigo-vera Fraseri,** nov. sp. f.

Fraser (1919) has reported the results of cultures from aecia on *Thalictrum dasycarpum* collected at Brandon, Manitoba. He obtained infection on *Elymus canadensis, E. virginicus,* and *Hordeum jubatum.* Negative results were obtained with *Agropyron tenerum, A. Richardsonii,* and *Triticum vulgare.*

This race is close to both *vulgaris* and *anomala,* but differs in that both *Elymus canadensis* and *E. virginicus* are susceptible species.

4. **Puccinia rubigo-vera circumscripta,** nov. sp. f.

Aecial hosts. — This race of *Puccinia rubigo-vera* was obtained on *Hordeum jubatum* from North Dakota (Th 9–9518) and Illinois (Th 33–27119). It produced aecia on *Thalictrum aquilegifolium, T. dasycarpum, T. dioicum,* and *T. paniculatum.* Pycnia were produced on *Thalictrum polygamum.*

Negative results were obtained with *Thalictrum angustifolium*, *T. minus*, and *T. minus adiantifolium*.

Grass hosts. — Only *Hordeum jubatum* was found to be favorable for this race.

Little or no infection was produced on *Agropyron caninum*, *A. pseudorepens*, *A. repens*, *A. Smithii*, *A. tenerum*, *Bromus carinatus*, *B. ciliatus*, *Elymus canadensis*, *E. condensatus*, *E. glaucus*, *E. robustus*, *E. virginicus*, *Hordeum Gussoneanum*, *H. murinum*, *H. nodosum*, *H. pusillum*, *H. vulgare*, *Hystrix Hystrix*, *Secale cereale*, *Sitanion Hystrix*, and *Triticum vulgare*.

This race is unique on account of its marked specialization to *Hordeum jubatum*.

5. Puccinia rubigo-vera hordeicola, nov. sp. f.

Aecial hosts. — The only culture (Th 24) of this race studied was derived from aecia on *Thalictrum Fendleri* collected by E. Bethel at Hot Springs, Colorado. Telia were not obtained on the grasses infected, and consequently information concerning the range of aecial hosts is not available.

Grass hosts. — *Hordeum jubatum* and *H. nodosum* proved to be the favorable grass hosts.

Negative results were obtained with *Agropyron caninum*, *A. repens*, *A. Smithii*, *A. tenerum*, *Elymus australis*, *E. canadensis*, *E. robustus*, *E. virginicus*, *Hordeum Gussoneanum*, *H. murinum*, *H. pusillum*, *H. vulgare*, *Hystrix Hystrix*, *Secale cereale*, and *Triticum vulgare*.

6. Puccinia rubigo-vera elymicola, nov. sp. f.

Aecial hosts. — The only culture (El 52) of this race was obtained from uredinia associated with telia (26019) which produced aecia on *Thalictrum dasycarpum*. The original collection was made on *Elymus canadensis* at Lafayette, Indiana.

This race was tested for aecial hosts only on *Thalictrum dasycarpum*, upon which it produced aecia. Probably it also will produce aecia on *Thalictrum dioicum*.

Grass hosts. — *Elymus canadensis*, *E. glaucus*, *E. robustus*, *E.*

striatus, E. virginicus, Hordeum Gussoneanum, and *Hystrix Hystrix* are the favorable grass hosts.

Negative results were obtained with *Agropyron caninum, A. Smithii, A. tenerum, Elymus condensatus, E. triticoides, Hordeum jubatum, H. murinum, H. vulgare, Secale cereale, Sitanion Hystrix, S. jubatum,* and *Triticum vulgare.*

This race has the widest host range on grasses of all the races so far studied from aecia on Thalictrum. It is, therefore, interesting to note that it is the only race on species of *Elymus* which did not also infect *Hordeum jubatum.*

7. **Puccinia rubigo-vera occidentalis,** nov. sp. f.

The only culture (El 11) of this race studied was obtained from uredinia collected by C. W. Hungerford on *Elymus glaucus* at Corvallis, Oregon. The rust was closely associated with aecia on a species of Thalictrum. Telia were not obtained in these studies, and the hosts for the aecial stage are, therefore, not known.

Grass hosts. — *Elymus canadensis, E. condensatus, E. glaucus, E. robustus,* and *Hordeum jubatum* proved to be favorable grass hosts. *Hordeum pusillum* was moderately susceptible.

Negative results were obtained with *Agropyron caninum, A. desertorum, A. intermedium, A. pseudorepens, A. repens, A. Smithii, A. tenerum, Bromus carinatus, B. japonicus, B. polyanthus, B. sitchensis, Elymus australis, E. virginicus, Hordeum murinum, H. nodosum, H. vulgare, Hystrix Hystrix, Secale cereale,* and *Triticum vulgare.*

8. **Puccinia rubigo-vera** sp. f. **alternans** (Arth.), nov. comb.
Puccinia alternans Arth. Mycologia, 1: 248–249. 1909.

Aecial hosts. — Arthur (1909) has shown that telia from *Bromus Porteri* (Coult.) Nash. collected at Ouray, Colorado, closely associated with aecia on *Thalictrum sparsiflorum* Turcz., produced aecia on *Thalictrum dioicum.* He states that E. W. D. Holway had collected a similar rust on *Bromus Pumpellianus* closely associated with aecia on Thalictrum at Banff, Alberta. To this rust Arthur gave the name *Puccinia alternans.* Though the aecia collected by E. Bethel at Pogosa Springs, Colorado, on *Thalictrum*

sp. (Th 81) were not sown on *Bromus Porteri*, it probably is the same rust as that studied by Arthur. If so the race produces aecia on *Thalictrum dioicum* and probably on *Thalictrum sparsiflorum*.

Grass hosts. — *Bromus carinatus*, *B. Porteri*, *B. Pumpellianus*, *B. Richardsonii*, and *B. sitchensis* are susceptible grass species.

Negative results were obtained with *Agropyron caninum*, *A. repens*, *A. tenerum*, *Bromus ciliatus*, *B. erectus*, *B. hordeaceus*, *B. inermis*, *B. japonicus*, *B. purgans*, *B. secalinus*, *B. sterilis*, *B. tectorum*, *B. vulgaris*, *Elymus canadensis*, *E. glaucus*, *E. virginicus*, *Hordeum jubatum*, *Secale cereale*, and *Triticum vulgare*. This race is sharply separated from all the preceding ones, since it is specialized to species of Bromus and does not infect any of the species of Elymus or Hordeum.

9. **Puccinia rubigo-vera** sp. f. **persistens** (Plowright), nov. comb.

Puccinia persistens Plowright. Mon. Brit. Ured. Ust., p. 181. 1889.

Puccinia dispersa sp. f. *Agropyri* Erikss. Ber. deut. bot. Gesell., 12:316. 1894.

Puccinia agropyrina Erikss. Ann. Sci. Nat., Eighth Ser., 9:273. 1889.

Plowright (1889) has shown that aecia from *Thalictrum flavum* are connected with rust on *Agropyron repens* (*Triticum repens*). To this he gave the name *Puccinia persistens*. Eriksson (1894) was not able to infect *Secale cereale* or *Triticum vulgare* with rust from *Agropyron repens* (*Triticum repens*). This he designated as a race *Agropyri* of *Puccinia dispersa*. He continued his studies (1899) and inoculated *Secale cereale*, *Triticum vulgare*, *Trisetum flavescens*, *Holcus lanatus*, *Bromus arvensis*, and *Agropyron repens* with rust from *Agropyron repens* and obtained abundant infection on *Agropyron repens*, occasionally slight infection on *Secale cereale* and *Bromus arvensis*, and negative results with the others. These results, taken with those obtained from rusts on Triticum, Secale, Trisetum, Holcus, and Bromus, led him to recognize the rusts on these various hosts as species, and he gave the name *Puccinia agropyrina* Erikss. to the rust of *Agropyron repens*.

Whether the rust connected by Plowright with aecia on Thalictrum and that studied by Eriksson are the same is difficult to determine. However, the results of the studies reported here agree so well with those of Plowright on the one hand and those of Eriksson on the other that it seems probable that one race is involved.

Aecial hosts. — Aecia of this race were produced on *Thalictrum Delavayi*, *T. flavum*, and *T. minus*. Only pycnia were produced on *T. angustifolium* and *T. aquilegifolium*.

Negative results were obtained with *Actaea alba*, *A. spicata*, *Aquilegia alpina*, *Aq. canadensis*, *Aq. chrysantha*, *Aq. coerulea*, *Aq. vulgaris*, *Clematis orientalis*, *C. virginiana*, *Echium vulgare*, *Hydrophyllum appendiculatum*, *Impatiens biflora*, *Phacelia tanacetifolia*, *Thalictrum dasycarpum*, *T. dioicum*, *T. paniculatum*, and *T. polygamum*.

Grass hosts. — The race is restricted, apparently, to *Agropyron repens* and probably *A. pseudorepens* for its grass hosts.

Species showing little or no infection are *Agropyron caninum*, *A. cristatum*, *A. desertorum*, *A. intermedium*, *A. Smithii*, *A. tenerum*, *Bromus carinatus*, *B. japonicus*, *B. tectorum*, *Elymus canadensis*, *E. robustus*, *E. virginicus*, *Hordeum jubatum*, *H. pusillum*, *H. vulgare*, *Hystrix Hystrix*, *Secale cereale*, and *Triticum vulgare*.

This race differs from all the preceding in both aecial and grass hosts. It more closely approaches the wheat race *Tritici*, infecting the same species of Thalictrum but differing in grass hosts. The material studied was collected in Minnesota and Wisconsin (Ag 10; 8818; Ag 30; 23019).

10. **Puccinia rubigo-vera** sp. f. **Tritici** (Erikss.) Carleton U.S. Dept. Agric., Div. Veg. Phy. Path., Bull. 16: 10. 1899.

    Puccinia dispersa sp. f. *Tritici* Erikss. Ber. deut. bot. Gesell., 12: 316. 1894.

    Puccinia triticina Erikss. Ann Sci. Nat., Eighth Ser., 9: 270. 1899.

Aecial hosts. — These studies would indicate that *Thalictrum Delavayi* and *T. flavum* are the most favorable species for the

development of the aecial stage of the race *Tritici* in the United States. Tochinai (1922) found *Thalictrum minus* var. *elatum* Lecoy to be very susceptible in Japan. The *Thalictrum minus* used in these studies only occasionally produced a few aecia and usually gave negative results. Ducomet (1925) obtained aecia on *Thalictrum glaucum* in France. This species has not been used sufficiently in these investigations to justify conclusions. Pycnia were obtained in one case and pycnia and aecia in another. Eremejava (1926) has shown that *Thalictrum flavum* (*T. exaltatum* Gaud.), *T. glaucum* Desf., *T. minus* (*T. ruthenicum* Fisch., *T. nutans* Gilib., *T. elatum* Jacq., *T. adiantifolium*), *T. lucidum* L., and *T. tuberosum* were very favorable hosts for the development of the aecia in Russia. *Thalictrum trigynum* Fisch., *T. cornellum* DC., *T. foetidum*, and *T. ambiguum* Schleich. showed slight development, whereas *T. angustifolium* and *T. aquilegifolium* only occasionally produced a few aecia.

In these investigations a few aecia have occasionally been produced on *Thalictrum angustifolium*, *T. aquilegifolium*, *T. dioicum*, *T. minus adiantifolium*, *T. polycarpum*, and *T. saxatile*. In most cases, however, either negative results or only pycnia were obtained on these species.

Aecia have not been obtained on *Thalictrum cultratum*, *T. dasycarpum*, *T. dipterocarpum*, *T. elegans*, *T. Fendleri*, *T. paniculatum*, *T. nutans*, *T. occidentale*, *T. simplex*, and *T. polygamum*. Only once have aecia been obtained outside the genus Thalictrum. One inoculation on *Anemonella thalictroides* gave pycnia and aecia. Four other collections, however, gave negative results on this species.

Whether the difference in the results obtained with *Thalictrum minus* and *T. glaucum* is significant remains to be seen. It may indicate groups within the race, specialized to different aecial hosts. It is possible that infection on *Anemonella thalictroides* and some of the North American species of Thalictrum may also be explained in this way.

Negative results have been obtained with *Aconitum Napellus*, *Actaea spicata*, *Anchusa officinalis*, *Anemone canadensis*, *A. cylindrica*, *A. vitifolia*, *Aquilegia alpina*, *Aq. canadensis*, *Aq. chrysantha*, *Aq. coerulea*, *Aq. eximia*, *Aq. pyrenaica*, *Aq. Skinneri*, *Aq. vulgaris*,

Cerinthe minor, Cimicifuga racemosa, Clematis Davidiana, C. flammula, C. Fremontii, C. Gouriana, C. grata, C. integrifolia, C. ligusticifolia, C. montana, C. ochroleuca, C. orientalis, C. paniculata, C. recta, C. virginiana, Cynoglossum officinale, Delphinium Geyeri, Echium vulgare, Hydrophyllum appendiculatum, H. virginianum, Impatiens biflora, Isopyrum biternatum, Mertensia virginica, Myosotis scorpoides, Phacelia californica, P. distans, P. tanacetifolia, Ranunculus aconitifolius, R. acris, and *Trollius europaeus.*

In addition, negative results have been reported by Eriksson (1899), Klebahn (1900), and Butler (1906) for *Achillea Ptarmica, Aconitum Lycoctonum, Aegopodium Podagraria, Agrostemma Githago, Anchusa arvensis, Anemone ranunculoides, Barbarea vulgaris, Berberis vulgaris, Campanula rotundifolia, Centaurea Cyanus, Coronaria floscuculi, Glechoma hederacea, Knautia arvensis, Launaea asplenifolia, Ligustrum vulgare, Lithospermum purpureo-coerulum, Lythrum Salicaria, Melandryum album, Myosotis arvensis, M. alpestris, Nasturtium sp., Nonnea rosea, Pastinaca sativa, Phillyrea sp., Prunella vulgaris, Pulmonaria officinalis, Ranunculus asiaticus, R. auricomus, R. bulbosus, R. Ficaria, R. flammula, R. lanuginosus, R. repens, Rhamnus cathartica, Ribes Grossularia, Rumex acetosa, Symphytum asperrimum, S. officinalis, Taraxacum officinale, Tussilage Farfara, Urtica dioica,* and *Valeriana dioica.*

Grass hosts. — Eriksson (1894, 1899) was the first to show that this rust is restricted to wheat. He inoculated *Agropyron repens, Bromus arvensis, B. brizaeformis, B. mollis, Holcus lanatus, Secale cereale,* and *Triticum vulgare* with urediniospores from *Triticum vulgare* and obtained good infection on *Triticum vulgare,* slight infection on *Secale cereale,* and negative results with the others. Consequently, Eriksson first considered this a race *Tritici* of *Puccinia dispersa* and later a species *Puccinia triticina.* In like manner, Carleton (1899) was able to infect wheat but had negative results with barley, oats, rye, *Agropyron Richardsonii, A. spicatum, A. tenerum, Dactylis glomerata, Elymus canadensis, E. canadensis glaucifolius,* and *E. virginicus.* Carleton considered the leaf rust of wheat a race *Tritici* of *Puccinia rubigo-vera.* Freeman and Johnson (1911) infected rye and barley to some extent, but were not able to infect oats.

The results reported here indicate that the race *Tritici*, taken as a whole, finds its most favorable hosts in *Triticum compactum*, *T. vulgare*, *T. spelta*, and *Aegilops crassa*. Strains resistant to some of the physiologic forms of the race probably occur in each of these species. *Triticum turgidum*, *T. polonicum*, *T. durum*, *T. dicoccum*, *T. dicoccoides*, *T. aegilopoides*, *Aegilops squarrosa*, *A. cylindrica*, and *A. ovata* are probably for the most part more or less resistant. Susceptible strains, however, do occur in these species. *Triticum monococcum* has so far been markedly resistant.

The following species gave negative results or showed only a trace of rust: *Agropyron caninum*, *A. cristatum*, *A. desertorum*, *A. pseudorepens*, *A. repens*, *A. Smithii*, *A. tenerum*, *Agrostis alba*, *A. stolonifera*, *A. perennans*, *A. verticillata*, *Alopecurus pratensis*, *Anthoxanthum odoratum*, *Arrhenatherum elatius*, *Bromus altissimus*, *B. brizaeformis*, *B. carinatus*, *B. ciliatus*, *B. erectus*, *B. hordeaceus*, *B. inermis*, *B. japonicus*, *B. Kalmii*, *B. mollis*, *B. polyanthus*, *B. Pumpellianus*, *B. Richardsonii*, *B. rubens*, *B. sitchensis*, *B. sterilis*, *B. tectorum*, *B. villosus*, *Elymus arkansanus*, *E. australis*, *E. canadensis*, *E. condensatus*, *E. glaucus*, *E. striatus*, *E. triticoides*, *E. virginicus*, *Festuca dumetorum*, *F. elatior*, *F. megalura*, *F. ovina*, *F. rubra*, *F. tenuiflora*, *Hordeum deficiens*, *H. distichon*, *H. Gussoneanum*, *H. intermedium*, *H. jubatum*, *H. murinum*, *H. nodosum*, *H. pusillum*, *H. vulgare*, *Hystrix Hystrix*, *Lolium multiflorum*, *L. temulentum*, *Secale cereale*, *S. montanum*, and *Sitanion Hystrix*.

The race *Tritici* may be further divided through the use of varieties of wheat as differential hosts. Thus Mains and Jackson (1926) were able to distinguish from the United States twelve physiologic forms (p. f. 1–12) by the reaction of eleven selected differential varieties of wheat. Scheibe (1928, 1930) has distinguished twelve physiologic forms (p. f. 11 and 13–23) from collections made in Germany, Latvia, Esthonia, Poland, Bulgaria, and Hungary. Wellenseik (1930) found three forms (p. f. 11, 14, and 15) in the Netherlands. Dodoff (1931) reports seven physiologic forms (p. f. 13, 15, 17, 19, 20, 21, and 24) from Bulgaria. Tscholakow (1931) reports six physiologic forms (p. f. 11, 13, 14, 17, 20, and 25) from Germany, the Netherlands, Austria, Hungary, and Bulgaria. In Australia Waterhouse (1929), using the same

series of wheat varieties, was able to distinguish only one physiologic form, which Johnston and Mains (1932) have denoted as p. f. 26. In North America twenty-seven additional forms have been distinguished since the original paper by Mains and Jackson, one (p. f. 27) by Johnston (1930), twenty-three (p. f. 28–50) by Johnston and Mains (1932), and three (p. f. 51–53) by Schall, Stakeman, and Levine (Johnston and Mains, 1932).

That at least some of the groups may be further divided by the use of additional differential varieties has been shown by both Waterhouse (1929) and Scheibe (1930). Waterhouse, using the differential varieties employed by Mains and Jackson, was able to distinguish only one physiologic form in Australia. The reactions of the variety Thew, however, showed that two physiologic forms occur there. These may be designated as p. f. 26–1 (Thew resistant) and p. f. 26–2 (Thew susceptible). Likewise, Scheibe has shown that p. f. 13 may be divided into three forms and p. f. 11 into five forms, by additional differential varieties of wheat. These may be designated as indicated for form 26.

By the use of the eight varieties of wheat, Malakoff C.I. 4898, Carina C.I. 3756, Brevit C.I. 3778, Webster C.I. 3780, Loros C.I. 3779, Mediterranean C.I. 3332, Hussar C.I. 4843, and Democrat C.I. 3384, fifty-three physiologic forms of the race *Tritici* have been recognized. Though some of these forms are rather simular and may not be distinct, such as 1 and 16, most of the physiologic forms are distinguished rather definitely by the reaction of one or more of the varieties. The following key and Tables V–X may be used to distinguish the various physiologic forms:

DIFFERENTIATION OF PHYSIOLOGIC FORMS OF *PUCCINIA RUBIGO-VERA TRITICI*

Malakoff resistant [3]
- Mediterranean resistant
  - Brevit resistant ..... Table V
  - Brevit susceptible ..... Table VI
- Mediterranean susceptible ..... Table VII

[3] Reactions of 0, 1, 2, and X are classified as resistant and those of 3 and 4 as susceptible. See Table IV for explanations of these types. By X is meant a reaction in which all types may be found on the same plant. Care should be taken not to confuse the results due to a mixture of physiologic forms.

Malakoff susceptible
Webster resistant..... Table VIII
Webster susceptible
Mediterranean resistant..... Table IX
Mediterranean susceptible..... Table X

e. Other races with aecia on Thalictrum

The following races have been shown to have aecia on species of Thalictrum and probably are to be considered races of *Puccinia rubigo-vera.* They are listed under the hosts infected.

Thalictrum alpinum — Agropyron violaceum

Arthur (1910) connected a rust on *Agropyron sp.* (*violaceum*) from Granby, Colorado, with aecia on *Thalictrum alpinum.* He did not obtain infection on *Thalictrum dioicum.* He first placed this in *Puccinia obliterata* and later included it with that species in *Dicaeoma Clematidis.*

Thalictrum minus — Agropyron cristatum

Tranzschel (1913) produced aecia on *Thalictrum minus* from telia on *Agropyron cristatum.* He discusses this under *Puccinia Elymi.* Since the teliospores were two-celled the rust apparently belongs in *Puccinia rubigo-vera.*

Thalictrum majus — Agropyron caninum

According to Sydow (1904), Liro connected a rust on *Agropyron caninum* with aecia on *Thalictrum majus.* Sydow discusses this under *Puccinia persistens.*

Thalictrum alpinum — Agrostis borealis

Juel (1894, 1896) obtained aecia on *Thalictrum alpinum* from telia on *Agrostis borealis. Thalictrum simplex* was not infected. *Agrostis borealis* inoculated with aeciospores from *Thalictrum alpinum* produced uredinia. Juel named this combination *Puccinia borealis.*

Thalictrum dioicum — Festuca Thuberi

Arthur (1916) inoculated *Anemone cylindrica, Aquilegia canadensis, Clematis ligusticifolia,* and *Thalictrum dioicum* from telia

TABLE V

PHYSIOLOGIC FORMS TO WHICH MALAKOFF, MEDITERRANEAN, AND BREVIT ARE RESISTANT

Differential varieties	Loros resistant				Loros susceptible					
	1	16	53	36	38	33	44	46	23	18
Malakoff	0	0	0	2–3	0	0	0	0–1	X	0
Carina	0	0	1	0	2–2+	1	2	2–3	4	4
Brevit	0	0	2	0–2	1–2	2+	2	2	2	2
Webster	0	0	1	0	0–1	0–1+	0–2	0–1	4	4
Loros	0	0	1	0–2	3–4	4	4	4	4	4
Mediterranean	1	0	0	2+	2+	2+	X	2	0	0
Hussar	1	2	3	1–2	1–2	1	0–1	1–2	4	4
Democrat	0	0	0	2+	2+	4	4	3–4	0	0

TABLE VI

PHYSIOLOGIC FORMS TO WHICH MALAKOFF AND MEDITERRANEAN ARE RESISTANT AND BREVIT IS SUSCEPTIBLE

Differential varieties	Carina resistant			Carina susceptible	
	11 *	51	14	22	26 †
Malakoff	0	0	0	X	0
Carina	2+	1	2–	4	4
Brevit	3–4	3	4	4	4
Webster	1–2	1	1	1–2	0
Loros	3–4	3	4	4	4
Mediterranean	1–2	2	0	0–1	0
Hussar	0–2	3	4	0–1	4
Democrat	0–2	3	0	0–1	0

* Scheibe (1930) has demonstrated that this is a group in which five forms may be differentiated by the use of additional varieties. These might be distinguished and designated as follows:

	p. f. 11–1	p. f. 11–2	p. f. 11–3	p. f. 11–4	p. f. 11–5
Poulard blanc lime 325	4	2	2	4	4
Peines Deficiance 326	4	4	1–2	4	1
Roter Tiroler Dinkel 335	1	1	4	1	1

† Waterhouse (1929) has shown that by the use of the variety Thew two forms may be recognized in this. They may be designated 26–1 (Thew resistant) and 26–2 (Thew susceptible).

TABLE VII

PHYSIOLOGIC FORMS TO WHICH MALAKOFF IS RESISTANT AND MEDITERRANEAN SUSCEPTIBLE

Differential varieties	Loros resistant					Loros susceptible			
	15	34	3	2	25	32	4	45	12
Malakoff	0	0	0–1	0–1	0	0	0–1	0	0
Carina	0	0	0–2	0–1	2	2	4	3–4	4
Brevit	0–1	0	2–2+	0–1	4	X	4	2+	4
Webster	0	0–1	0–2	0	0	1–2	1	4	1
Loros	0–1	1	2–4	0–1	2	3–4	3–4	4	4
Mediterranean	4	4	3–4	4	4	4	3–4	3–4	4
Hussar	0–1	X	0–1	3–4	0	1–2	2–2+	2	4
Democrat	4	4	4	4	4	4	1–2	3–4	4

TABLE VIII

PHYSIOLOGIC FORMS TO WHICH MALAKOFF IS SUSCEPTIBLE AND WEBSTER RESISTANT

Differential varieties	Mediterranean resistant *						Mediterranean susceptible					
	17	37	50	29	43	49	5	52	39	28	40	6
Malakoff	4	3–4	4	4	4	4	4	4	3–4	4	4	4
Carina	0	2+	2	2–3	3	3	0	0	2–3	1+	4	2
Brevit	0	2	4	2–3	3	3	0–1	1	2–3	1+	2	4
Webster	0	0–2	2–	2–3	1–2	2	0–1	0	0–1	2+	0	1–2
Loros	0	3–4	3	4	4	3–4	0–1	1	4	3	3–4	3
Mediterranean	0	2+	0	1–2+	1	0	4	4	3–4	4	4	3–4
Hussar	4	2	2	3	2	4	0–2	3	0–1	3	4	3
Democrat	0	2+	0	1	1–2	0	4	4	3–4	4	2–3	3–4

* See also p. f. 36 in Table V.

TABLE IX

PHYSIOLOGIC FORMS TO WHICH MALAKOFF AND WEBSTER ARE SUSCEPTIBLE AND MEDITERRANEAN IS RESISTANT

Differential varieties	Hussar resistant *						Hussar susceptible †			
	9	27	41	19	47	10	31	13 ‡	24	20
Malakoff	4	3–4	4	4	4	4	4	4	4	4
Carina	1–2	2	2–3	4	3	4	2	4	3–4	4
Brevit	1–2	1–2	2	2	2	4	1–2	2–	1–2	4
Webster	4	3–4	4	4	4	4	4	4	4	4
Loros	4	3	4	4	0	4	4	4	4	4
Mediterranean	0–1	2	2	0	2	1–2	1–2	0	0–2	0
Hussar	1–2+	2–3	2	1	0	1–2	3–4	4	4	4
Democrat	0–1	2–3	3–4	0	2	1–2	1–2	0	X	0

* See also p. f. 48 in Table X.

† See also p. f. 29 in Table VIII.

‡ Scheibe (1930) has demonstrated that this is a group which may be divided into three forms. They might be distinguished and designated as follows: Probsteier 364 resistant (0), Tiroler Dinkel 335 resistant (0–1) p. f. 13 1; Probsteier susceptible (4), Tiroler Dinkel resistant (0) p. f. 13–2; Probsteier susceptible (4), Tiroler Dinkel susceptible (4) p. f. 13-3.

TABLE X

PHYSIOLOGIC FORMS TO WHICH MALAKOFF, WEBSTER, AND MEDITERRANEAN ARE SUSCEPTIBLE

Differential varieties	Democrat resistant		Democrat susceptible				
	8	48	7	35	30	42	21
Malakoff	4	4	4	4	4	4	4
Carina	1	3–4	1–2	2+	2–3	2–3	4
Brevit	4	2	1	2+	2–3	3	2
Webster	4	4	4	4	3	4	4
Loros	4	4	1	4	3–4	4	4
Mediterranean	3–4	2–3	4	4	4	3–4	4
Hussar	1	2	1	1	1–2+	4	4
Democrat	1	0	4	4	4	4	4

INDEX TO PHYSIOLOGIC FORMS OF THE RACE *TRITICI*

p. f.	Table	p. f.	Table	p. f.	Table
1	V	19	IX	37	VIII
2	VII	20	IX	38	V
3	VII	21	X	39	VIII
4	VII	22	VI	40	VIII
5	VIII	23	V	41	IX
6	VIII	24	IX	42	X
7	X	25	VII	43	VIII
8	X	26	VI	44	V
9	IX	27	IX	45	VII
10	IX	28	VIII	46	V
11	VI	29	VIII	47	IX
12	VII	30	X	48	X
13	IX	31	IX	49	VIII
14	VI	32	VII	50	VIII
15	VII	33	V	51	VI
16	V	34	VII	52	VIII
17	VIII	35	X	53	V
18	V	36	V		

on *Festuca Thuberi* collected at Lake Eldora, Colorado. Accia were obtained only on *Thalictrum dioicum*. According to Arthur, Bethel also obtained aecia on *Thalictrum Fendleri* with this rust. Arthur first included this in "*Puccinia Agropyri* (*P. alternans*)." Later (1919) he separated it under the name *Puccinia Cockerelliana*.

Thalictrum spp. — Poa nemoralis firmula

Fischer (1898) found telia on *Poa nemoralis firmula* associated with aecia on *Thalictrum minus*. He inoculated *Thalictrum aquilegifolium*, *T. minus*, *T. foetidum*, and *Aquilegia vulgaris*. Aecia developed on all species of Thalictrum (only to slight extent on *T. foetidum*). Fischer considered this rust *Puccinia persistens*.

Thalictrum foetidum — Trisetum distichophyllum

Fischer and Mayor (1924) inoculated *Thalictrum foetidum*, *T. glaucum*, *T. palmatum*, *T. aquilegifolium*, *T. minus*, and *T. flavum* from teliospores from *Trisetum distichophyllum*. They obtained a good development of aecia on *Thalictrum foetidum*, slight development on *T. glaucum* and *T. palmatum*, and negative results with

the other three species. They described this rust as *Puccinia Thalictri-distichophylli.*

f. Relationship of Puccinia Elymi and P. tomipāra

Westendorp (1851) described a rust on *Elymus arenarius* from near Ostend under the name *Puccinia Elymi.* He noted that the teliospores were two-celled. Lagerheim (1889) states that he examined the type material and that most of the teliospores were three-celled in a linear series. He concludes that Westendorp apparently mistook the lower cell for a pedicel. Lagerheim considered the multicellular character of the teliospores of sufficient importance to distinguish a genus, which he named *Rostrupia.* As has been pointed out by several investigators, it is doubtful whether this is sufficient for generic separation. If it is a fixed character, however, it would appear to be a good specific difference.

Without question *Puccinia Elymi* is closely related to *Puccinia rubigo-vera,* as is shown by its host specialization. Rostrup (1898) noted aecia on *Thalictrum minus* closely associated with telia of *Puccinia Elymi.* By inoculating with aeciospores from the Thalictrum he obtained uredinia on *Elymus arenarius.* Tranzschel (1914) obtained aecia on *Thalictrum minus* by inoculations from telia of *Puccinia Elymi* on *Elymus sp.* Tranzschel also reports a rust on *Agropyron cristatum* with three-celled teliospores, with which he obtained aecia on *Thalictrum minus.*

Puccinia tomipara is a name given by Trelease (1886) to a rust on *Bromus ciliatus.* The teliospores of this rust are described as 2–5-celled, commonly 3–4-celled, with the uppermost septum oblique or not infrequently parallel to the axis of the spore. Fraser (1911) has shown that *Puccinia tomipara* from *Bromus ciliatus* and *B. latiglumis* is connected with aecia on *Thalictrum dasycarpum.* He believes that the many-celled condition of the teliospores is a fixed character.

It is evident that there is a remarkable parallelism between these two rusts and races of *Puccinia rubigo-vera.* However, before their actual relationship and position can be determined they should at least be cultured from telia through aecia and back to telia, and information should be obtained concerning the

stability of the multicellular condition of the teliospores. If this is unstable and they revert to the two-celled condition, they should, probably, be included as races in *Puccinia rubigo-vera*. If it is stable, they should be kept apart as distinct species. For the present it seems best so to treat them.

B. AECIA ON SPECIES OF CLEMATIS

a. Results obtained from inoculations from telia on grasses to aecial hosts

Aecia were produced on species of Clematis by inoculating from teliospores collected on species of Agropyron, Bromus, Elymus, and Hystrix. The results obtained are as follows:

Telia collected on species of Agropyron

18720. Overwintered telia collected on *Agropyron sp.*, April 11, 1921, at Manitou, Colorado, by E. Bethel, were sown on *Thalictrum Fendleri* and *Clematis ligusticifolia*, with production of pycnia and aecia on the latter only.

18820. Overwintered telia collected on *Agropyron tenerum*, April 11, 1921, at Manitou, Colorado, by E. Bethel, were sown on *Clematis flammula*, *C. Fremontii* S. Wats., *C. integrifolia*, *C. lasiantha*, *C. ligusticifolia*, *C. orientalis* L., *C. paniculata*, *C. recta*, and *C. virginiana*, with production of pycnia and aecia on *C. ligusticifolia* only.

9921. Collected on *Agropyron Smithii molle*, Sept. 3, 1921, at Ignacia, Colorado, by E. Bethel. This was sown on *Clematis ligusticifolia*, with production of pycnia and aecia.

These cultures would indicate that there is a western race on species of Agropyron, which is probably closely restricted to *Clematis ligusticifolia* for its aecial host.

Telia collected on species of Bromus

6818. Collected on *Bromus ciliatus*, Sept. 19, 1918, at Cornell, Wisconsin, by J. J. Davis. This was sown on *Anemone canadensis*, *A. cylindrica*, *Aquilegia canadensis* L., *Clematis virginiana*, *Delphinium Geyeri* Greene, *Hydrophyllum appendiculatum* Michx.,

Impatiens biflora, and *Thalictrum dioicum*, with production of pycnia and aecia on *Clematis virginiana* only.

7218. Collected on *Bromus Kalmii*, Oct., 1918, at Madison, Wisconsin, by H. S. Jackson. This was sown on *Anemone canadensis*, *A. cylindrica*, *Aquilegia canadensis*, *Clematis virginiana*, and *Hydrophyllum appendiculatum*, with production of pycnia and aecia on *Clematis virginiana* only.

25819. Telia developed in the greenhouse on *Bromus ciliatus* as the result of inoculations from aecia on Clematis collected June 18, 1919, at Lewis, New York, by L. H. Pennington. (See culture C 13.) These telia were sown on *Clematis virginiana* and *Thalictrum dioicum*, producing pycnia and aecia on *C. virginiana* only.

18920. Overwintered telia collected on *Bromus Porteri* (Coult.) Nash., April 11, 1921, at Manitou, Colorado, by E. Bethel, were sown on *Clematis Douglasii* Hook., *C. integrifolia*, *C. lasiantha*, *C. ligusticifolia*, *C. orientalis*, *C. paniculata*, *C. recta*, *C. virginiana*, and *Thalictrum Fendleri*, producing pycnia and aecia on *C. ligusticifolia* and *C. virginiana*.

19420. Overwintered telia collected on *Bromus ciliatus*, April 23, 1921, at Battle Ground, Indiana, by the writer, were sown on *Clematis virginiana* and *Thalictrum dioicum*, with production of pycnia and aecia on *C. virginiana* only.

Telia collected on species of Elymus

6018. Collected on *Elymus sp.*, Aug. 23, 1918, at Ithaca, New York, by H. S. Jackson. See Table XI for results.

12218. Collected on *Elymus canadensis*, Nov., 1918, at Denver, Colorado, by H. S. Jackson. See Table XI.

12318. Collected on *Elymus canadensis*, Nov. 12, 1918, at Denver, Colorado, by H. S. Jackson. See Table XI.

12418. Collected on *Elymus canadensis*, Nov., 1918, at Denver, Colorado, by H. S. Jackson. See Table XI.

12918. Collected on *Elymus canadensis*, Nov., 1918, at Denver, Colorado, by H. S. Jackson. See Table XI.

13518. Collected on *Elymus canadensis*, Nov., 1918, at Denver, Colorado, by H. S. Jackson. See Table XI.

TABLE XI

RESULTS OBTAINED FROM INOCULATIONS WITH SOME COLLECTIONS OF *PUCCINIA RUBIGO-VERA* HAVING AECIA ON *CLEMATIS VIRGINIANA* *

Species inoculated	6018†	12218	12318	12418	12918	13518
Aconitum Napellus	—	..	—	..	..	—
Actaea alba	—	..	—	..	..	..
rubra	..	..	—	..	..	..
spicata	..	..	—	..	..	..
Anemone canadensis	—	—	—	..	—	..
cylindrica	..	—	—	—	—	—
virginiana	..	..	—	—	..	..
Aquilegia canadensis	—	—	—	..	—	—
chrysantha	—	..	—	..	..	..
coerulea	—	—	—	—	—	..
glandulosa	—	..	..	..	..	..
vulgaris	—	..	..	..	..	..
Cimicifuga racemosa	..	..	—	..	..	..
Clematis Douglasii	—	..	—	—	—	..
Fremontii	—	..	—	—	—	..
Heraclaefolia	—	..	..	—	..	..
orientalis	—	..	0	0	..	..
recta	—	..	..	0	..	..
Scottii	—	..	—	—	—	..
virginiana	0I	0I	0I	0I	0I	0I
Delphinium Geyeri	..	—	—	—	—	—
Echium vulgare	..	—	—	..	..	—
Hydrophyllum appendiculatum	—	—	—	..	—	—
Impatiens biflora	..	—	—	..	—	..
Mertensia virginica	..	..	—	..	..	..
Myosotis palustris	..	—	—	..	..	—
Phacelia californica	..	—	—	..	—	—
distans	..	..	..	..	—	..
Ranunculus cymbalaria	—	..	—	..	..	..
repens	—	..	..	..	..	..
Thalictrum aquilegifolium	—	..	—	..	—	..
dasycarpum	..	..	..	..	—	..
dioicum	..	—	—	..	..	—
occidentale	..	..	..	—	..	..
Trollius europaeus	..	..	—	..	..	..

* For other results see text.

† Accession numbers of collections. For data see text.

14818. Collected on *Elymus virginicus*, Nov. 25, 1918, at Evansville, Indiana, by the writer. This was sown on *Anemone canadensis*, *A. cylindrica*, *Aquilegia canadensis*, *Clematis orientalis*, *C. virginiana*, *Hydrophyllum appendiculatum*, *Impatiens biflora*, *Myosotis palustris*, and *Thalictrum occidentale*, with production of pycnia on *C. orientalis* and pycnia and aecia on *C. virginiana*.

15318. Collected on *Elymus virginicus*, Nov. 28, 1918, at Mt. Vernon, Indiana, by L. S. Cheney. This was sown on *Actaea alba*, *Anemone canadensis*, *Aquilegia coerulea* James, *Clematis Douglasii*, *C. virginiana*, *Impatiens biflora*, and *Thalictrum occidentale*, with production of pycnia and aecia on *C. virginiana* only.

16419. Collected on *Elymus virginicus*, Aug. 25, 1919, at New Haven, Indiana, by L. S. Cheney. This was sown on *Clematis virginiana*, *Impatiens biflora*, and *Thalictrum dioicum*. Pycnia and aecia were produced on *Clematus virginiana* and *Impatiens biflora*. This indicates a mixture of races on *Elymus virginicus*.

22719. Collected on *Elymus canadensis*, Oct. 18, 1919, at Manitou, Colorado, by E. Bethel. Sown on *Clematis Davidiana*, *C. Douglasii*, *C. Fremontii*, *C. lanuginosa* Lindl., *C. lasiantha*, *C. ligusticifolia*, *C. orientalis*, *C. paniculata*, *C. recta*, *C. Scottii* Porter, *Hydrophyllum appendiculatum*, and *Thalictrum occidentale*, with production of pycnia on *C. Davidiana* and *C. orientalis* and pycnia and aecia on *C. lanuginosa* and *C. ligusticifolia*.

23219. Collected on *Elymus canadensis*, Sept. 19, 1919, at Colorado Springs, Colorado, by E. Bethel. This was sown on *Anemone cylindrica*, *Clematis Davidiana*, *C. lasiantha*, *C. virginiana*, and *Thalictrum dasycarpum*, with production of pycnia and aecia on *C. virginiana* only.

25019. Collected on *Elymus canadensis*, Oct. 18, 1919, at Garden of the Gods, Colorado, by E. Bethel. This was sown on *Aquilegia canadensis*, *Clematis virginiana*, *Hydrophyllum appendiculatum*, and *Thalictrum dasycarpum*, with production of pycnia and aecia on *C. virginiana* only.

3420. Collected on *Elymus condensatus*, June 13, 1920, at Monrovia, California, by E. Bethel. This was sown on *Anemone canadensis*, *Clematis ligusticifolia*, *Delphinium Nelsonii* Greene,

Phacelia californica, *P. distans*, and *Thalictrum dioicum*, with production of pycnia and aecia on *Clematis ligusticifolia* only.

3520. Collected on *Elymus condensatus*, June 19, 1920, at Monrovia, California, by E. Bethel. This collection was sown on *Clematis Douglasii*, *C. ligusticifolia*, and *Phacelia distans*, with production of pycnia and aecia on *Clematis ligusticifolia* and *Phacelia distans*. The collection evidently was a mixture of two races.

5320. Collected on *Elymus triticoides* Buckley, July 8, 1920, at San Diego, California, by E. Bethel. This was sown on *Anemone cylindrica*, *Clematis Douglasii*, *C. ligusticifolia*, *Delphinium Nelsonii*, *D. Penardi* Huth., *Onosmodium sp.*, *Phacelia californica*, *P. distans*, and *Thalictrum occidentale*, with production of aecia on *C. ligusticifolia* only.

7120. Collected on *Elymus triticoides*, July 11, 1920, at Warner's Hot Springs, California, by E. Bethel. This was sown on *Cynoglossum officinale*, *Clematis ligusticifolia*, *Onosmodium sp.*, *Phacelia californica*, *P. distans*, and *Thalictrum occidentale*, with production of pycnia and aecia on *C. ligusticifolia* only.

7220. Collected on *Elymus condensatus*, July 11, 1920, at Warner's Hot Springs, California, by E. Bethel. This was sown on *Clematis ligusticifolia*, *Delphinium Geyeri*, *Phacelia californica*, and *P. distans*, with production of pycnia and aecia on *Clematis ligusticifolia* only.

11120. Collected on *Elymus sp.*, Aug. 21, 1920, at Berkeley, California, by E. Bethel. This was sown on *Clematis Douglasii*, *C. ligusticifolia*, *C. paniculata*, *C. recta*, *C. virginiana*, *Phacelia distans*, *and Thalictrum dioicum*, with production of aecia on *C. ligusticifolia* and *C. virginiana*.

19020. Overwintered telia on *Elymus canadensis* were collected, April 11, 1921, at Manitou, Colorado, by E. Bethel. They were sown on *Clematis Davidiana* and *C. ligusticifolia*, with production of pycnia and aecia on *C. ligusticifolia* only.

Telia collected on *Hystrix Hystrix*

17320. Collected on *Hystrix Hystrix*, Aug. 19, 1920, at Ulsterville, New York, by P. Wilson. This was sown on *Actaea alba*,

Cimicifuga racemosa (L.) Nutt., *Clematis virginiana*, *Delphinium Consolidum* L., and *Impatiens biflora* with production of pycnia and aecia on *Clematis virginiana*.

b. Results obtained from inoculations from aecia on Clematis to various species of grasses

In a number of inoculations the aecia obtained on Clematis were sown on a series of species of grasses. In a few the uredinia, associated with telia which produced aecia, were studied in like manner. The following collections have been studied with the results given in Tables XII–XV:

C 1. From aecia collected on *Clematis virginiana*, July 15, 1918, at Ithaca, New York, by H. H. Whetzel.

C 3. From aecia on *Clematis virginiana* produced by inoculation with collection 6018 from *Elymus sp.*

C 4. From aecia on *Clematis virginiana* produced by inoculation with collection 15318 from *Elymus virginicus.*

C 6. From aecia on *Clematis virginiana* produced by inoculation with collection 6018 from *Elymus sp.*

C 8. From aecia on *Clematis virginiana* produced by inoculation with collection 6818 from *Bromus ciliatus.*

C 9. From aecia on *Clematis virginiana* produced by inoculation with collection 12418 from *Elymus canadensis.*

C 11. From aecia collected on *Clematis sp.*, June 1, 1919, at Corvallis, Oregon, by G. R. Hoerner.

C 13. From aecia collected on *Clematis sp.* (probably *virginiana*), June 18, 1919, at Lewis, New York, by L. H. Pennington.

C 14. From aecia collected on *Clematis ligusticifolia*, June 20, 1919, at Boulder, Colorado, by E. Bethel.

C 16. From aecia collected on *Clematis sp.* (probably *virginiana*), June 23, 1919, at Charlottesville, Virginia, by A. G. Johnson.

C 17. From aecia on *Clematis sp.* from unknown source.

C 19. From aecia collected on *Clematis sp.*, June 16, 1919, at Manitou Springs, Colorado, by G. H. Coons. The host is probably *Clematis ligusticifolia*, the common species of Colorado.

TABLE XII

REACTION OF SPECIES OF GRASSES TO RACES *ORIENTALIS*, *VIRGINICA*, *INDIANENSIS*, AND *BETHELI* OF *PUCCINIA RUBIGO-VERA* HAVING AECIA ON CLEMATIS

Species inoculated	Race orientalis					Race virginica	Race indianensis	Race Betheli
	C 1*	C 3	C 6	C 16	C 38	C 30	C 4	C 9
Agropyron caninum	+	+	+	+	t	−	t	t
cristatum	..	−	..	−	..	−	..	-
desertorum	..	−	..	..	..	..	..	..
intermedium	..	−	..	..	..	..	..	..
pseudorepens	..	−	..	..	..	..	..	t
repens	−	−	−	−	−	−	−	−
Smithii	−	−	−	−	−	−	−	−
tenerum	−	−	−	−	t	−	t	−
Bromus carinatus	..	−	−	−	..	..	..	−
ciliatus	..	−	−	−	−	−	−	−
erectus	..	..	..	..	..	..	−	..
japonicus	−	..	..	..	..	..	−	..
Kalmii	..	−	−	−	..	..	−	..
polyanthus	..	−	−	..	..	..	−	−
pratensis	..	..	..	..	..	..	−	..
sitchensis	..	..	..	..	..	..	−	..
sterilis	..	−	..	.	..	..	..	..
tectorum	−	..	−	..	..	..	..	−
vulgaris	..	..	..	..	..	..	−	..
Elymus arkansanus	..	++	+	..	..	..	t	−
australis	..	t	+	+	..	..	−	−
canadensis	+	t	+	+	−	+	+++	+++
condensatus	..	..	−	..	..	t	..	−
glaucus	..	+	+	t	+	−	−	+
robustus	+	t	−	+	..	..	..	t
virginicus	+++	+++	+++	+++	+++	+++	+++	+
Hordeum Gussoneanum	..	++	++	..	+	..	..	++
jubatum	++	+++	++	+++	+++	+	++	+
murinum	..	t	−	−	..	..	..	t
nodosum	..	t	+	−	+	−	..	t
pusillum	+	t	t	t	t	−	..	+
vulgare	t	−	−	−	..	..	..	−
Hystrix Hystrix	++	+++	++	+++	+++	−	++	t
Secale cereale	−	−	−	−	..	..	..	−
Sitanion Hystrix	..	+	+	t	−	..	..	−
Triticum vulgare	−	−	t	−	−	−	..	−
Trisetum spicatum	..	−	..	..	..	..	..	..

* For data concerning source of cultures see text.

TABLE XIII

REACTIONS OF SPECIES OF GRASSES TO RACES *COLORADENSIS* AND *CALIFORNICA* OF *PUCCINIA RUBIGO-VERA* HAVING AECIA ON CLEMATIS

Species inoculated	Race coloradensis		Race californica	
	C 26 *	C 41	C 32	C 34
Agropyron caninum	−	−	+	+
cristatum	−	..	−	−
repens	−	−	−	−
Smithii	−	−	−	−
tenerum	−	−	−	−
Bromus ciliatus	−	..	−	−
Elymus arkansanus	−	..	..	..
australis	−	..	..	..
canadensis	+++	+++	−	−
condensatus	..	+	+++	+++
glaucus	−	−	..	−
virginicus	+++	+++	−	−
Hordeum Gussoneanum	..	−	−	−
jubatum	−	−	−	−
murinum	−	..	..	..
nodosum	−	..	−	−
pusillum	−	..	−	..
vulgare	−	..	..	−
Hystrix Hystrix	−	..	−	−
Secale cereale	−	..	..	..
Sitanion Hystrix	−	..	−	−
Triticum vulgare	−	..	+	t

* For data concerning source of cultures see text.

TABLE XIV

REACTIONS OF SPECIES OF GRASSES TO COLLECTIONS OF RACES *CLEMATICOLA*, *OREGONENSIS*, AND *MONTANENSIS* OF *PUCCINIA RUBIGO-VERA* HAVING AECIA ON CLEMATIS

Species inoculated	Race clematicola			Race oregonensis		Race montanensis
	C 14 *	C 17	C 19	El 28	El 30	C 44
Agropyron caninum	t	–	–	–	–	..
cristatum	–	..	..	–	..	..
desertorum	..	..	..	–	..	..
intermedium	–	..	..	..	..	..
repens	–	..	–	–	..	..
Smithii	–	..	–	–	..	–
tenerum	–	–	–	–	–	+++
Bromus carinatus	–	–	–	..	..	..
ciliatus	–	–	–	..	..	..
Kalmii	..	–	–	..	..	..
polyanthus	..	..	–	..	..	..
Elymus australis	–	..	t	..	–	..
canadensis	–	–	–	–	..	–
condensatus	–	..	..	–	t	–
glaucus	+++	..	+++	+++	+++	–
robustus	–	t	–	–	–	..
virginicus	t	–	–	–	..	–
Hordeum Gussoneanum	+++	++	++	–	–	++
jubatum	t	t	t	+++	+++	–
murinum	–	–	–	–	..	..
nodosum	–	..	–	..	–	..
pusillum	t	t	–	t	–	..
vulgare	–	t	t	–	..	..
Hystrix Hystrix	t	–	–	–	–	–
Secale cereale	..	–	–	–	..	..
Sitanion Hystrix	–	–	–	+	–	–
Triticum vulgare	t	–	–	..	t	..

* For data concerning source of cultures see text.

TABLE XV

REACTIONS OF SPECIES OF GRASSES TO COLLECTIONS OF RACES *ARTHURI* AND *BROMICOLA* OF *PUCCINIA RUBIGO-VERA* HAVING AECIA ON CLEMATIS

Species inoculated	Race Arthuri				Race bromicola
	C 8 *	C 13	C 29	C 35	C 11
Agropyron caninum	–	–	..	–	–
cristatum	–	..	..	–	–
desertorum	..	..	..	..	–
intermedium	–	..	..	..	–
pseudorepens	–	..	..	..	–
repens	–	–	..	–	–
Smithii	–	–	..	–	–
tenerum	–	–	..	–	–
Bromus altissimus	–	–	t	..	–
carinatus	t	–	–	..	+++
ciliatus	+++	+++	+++	+++	–
erectus	–	–	..	..	–
hordeaceus	–	–	..	..	–
inermis	–	–	–	..	–
japonicus	–	–	–	..	–
Kalmii	t	t	–	..	t
mollis	–	–	..	..	..
polyanthus	–	–	..	..	+++
pratensis	–	–	..	..	–
purgans	..	..	+++	..	..
secalinus	–	–	..	..	–
sitchensis	–	–	..	..	+++
sterilis	–	–	..	..	–
tectorum	–	–	..	..	–
villosus	–	..	..	..	–
Elymus arkansanus	..	..	..	..	–
australis	–	–	..	..	–
canadensis	–	–	..	–	–
condensatus	–	..	..	..	–
glaucus	–	..	..	–	–
robustus	–	–	..	..	–
virginicus	–	–	..	–	–
Hordeum Gussoneanum	–	..	..	..	..
jubatum	–	–	..	–	–
murinum	–	–	..	..	–
nodosum	–	–	..	..	–
pusillum	–	–	..	..	–
vulgare	..	..	..	..	–
Hystrix Hystrix	–	–	..	..	–
Secale cereale	–	–	..	..	–
Sitanion Hystrix	–	–	..	–	–
Triticum vulgare	–	–	..	..	–

* For data concerning source of cultures see text.

C 26. From aecia on *Clematis ligusticifolia* produced by inoculation with collection 22719 from *Elymus canadensis.*

C 29. From aecia on *Clematis virginiana* produced from collection 25819 from *Bromus ciliatus.*

C 30. From aecia on *Clematis virginiana* produced from collection 16419 from *Elymus virginicus.*

C 32. From aecia on *Clematis ligusticifolia* produced from collection 3520 from *Elymus condensatus.*

C 34. From aecia on *Clematis ligusticifolia* produced from collection 7220 from *Elymus condensatus.*

C 35. From aecia on *Clematis sp.* from unknown source.

C 38. From aecia on *Clematis virginiana* produced from collection 17320 from *Hystrix Hystrix.*

C 41. From aecia on *Clematis ligusticifolia* produced from collection 19020 from *Elymus canadensis.*

C 44. From aecia collected on *Clematis sp.*, Aug., 1921, at Bozeman, Montana, by E. H. Toole.

El 28. From uredinia on *Elymus sp.* produced by inoculation by G. R. Hoerner from aecia on *Clematis sp.* at Corvallis, Oregon, in 1919.

El 30. From uredinia on *Elymus sp.* produced by inoculation by G. R. Hoerner from aecia on *Clematis sp.* at Corvallis, Oregon, in June, 1919.

Vi 1. From aecia collected on *Clematis* (*Viorna*) *Douglasii*, June 26, 1919, at Steamboat Springs, Colorado, by E. Bethel; uredinia were obtained on *Hordeum jubatum.*

c. Summary of races of Puccinia rubigo-vera with aecia on species of Clematis

A series of races somewhat similar to those reported with aecia on Thalictrum have been distinguished within the group having aecia on Clematis. The following races have been recognized:

11. Puccinia rubigo-vera orientalis, nov. sp. f.

Aecial hosts. — This race of *Puccinia rubigo-vera* produces its aecia on *Clematis virginiana.*

Negative results were obtained with *Aconitum Napellus*, *Actaea*

alba, Anemone canadensis, Aquilegia canadensis, Aq. chrysantha, Aq. coerulea, Aq. glandulosa, Aq. vulgaris, Cimicifuga racemosa, Clematis Douglasii, C. Fremontii, C. Heraclaefolia, C. orientalis, C. recta, C. Scottii, Hydrophyllum appendiculatum, Ranunculus Cymbalaria, R. repens, and *Thalictrum aquilegifolium.*

Grass hosts. — *Elymus virginicus, Hordeum jubatum,* and *Hystrix Hystrix* are favorable species of grasses. *Elymus arkansanus* and *Hordeum Gussoneanum* were moderately susceptible.

Negative results were obtained or only slight infection occurred with *Agropyron caninum, A. cristatum, A. desertorum, A. intermedium, A. pseudorepens, A. repens, A. Smithii, A. tenerum, Bromus carinatus, B. ciliatus, B. japonicus, B. Kalmii, B. polyanthus, B. sterilis, B. tectorum, Elymus australis, E. canadensis, E. condensatus, E. glaucus, E. robustus, Hordeum murinum, H. nodosum, H. pusillum, H. vulgare, Secale cereale, Sitanion Hystrix, Triticum vulgare,* and *Trisetum spicatum.*

This race apparently is fairly prevalent in the eastern United States. It has been collected (C 1, C 3–6018, C 6–6018, C 16, C 38–17320) in New York and Virginia.

12. **Puccinia rubigo-vera virginica,** nov. sp. f.

Aecial hosts. — This race produces pycnia and aecia on *Clematis virginiana.* Only one other species, *Thalictrum dioicum,* was inoculated; it gave negative results.

Grass hosts. — Only *Elymus virginicus* has been found to be susceptible.

Negative results or at the most only slight development of uredinia occurred on *Agropyron caninum, A. cristatum, A. repens, A. Smithii, A. tenerum, Bromus ciliatus, Elymus canadensis, E. condensatus, E. glaucus, Hordeum jubatum, H. nodosum, H. pusillum, Hystrix Hystrix,* and *Triticum vulgare.*

Only one collection (C 30–16419) of this race from *Elymus virginicus,* from Indiana, has been studied.

13. **Puccinia rubigo-vera indianensis,** nov. sp. f.

Aecial hosts. — *Clematis virginiana* is also the susceptible species for the aecial stage of this race.

Negative results were obtained with *Actaea alba*, *Anemone canadensis*, *Aquilegia coerulea*, *Clematis Douglasii*, *Impatiens biflora*, and *Thalictrum occidentale*.

Grass hosts. — *Elymus canadensis*, *E. virginicus*, and *Hordeum jubatum* are the favorable species of grasses. *Hystrix Hystrix* was moderately susceptible.

Negative results or only a few, small uredinia were obtained with *Agropyron caninum*, *A. repens*, *A. Smithii*, *A. tenerum*, *Bromus ciliatus*, *B. erectus*, *B. japonicus*, *B. Kalmii*, *B. polyanthus*, *B. pratensis*, *B. sitchensis*, *B. vulgaris*, *Elymus arkansanus*, *E. australis*, and *E. glaucus*.

Only one specimen (C 4–15318) was studied from *Elymus virginicus;* it was collected in Indiana.

14. **Puccinia rubigo-vera Betheli,** nov. sp. f.

Arthur (1915) reports connecting a rust on *Elymus canadensis* with aecia on *Clematis ligusticifolia*. The rust on *Elymus canadensis* was obtained by E. Bethel as a result of inoculation with aeciospores from aecia collected on *Clematis ligusticifolia* at Boulder, Colorado. Arthur was not able to infect *Anemone cylindrica*, *Clematis Douglasii*, *Delphinium Geyeri*, *Hydrophyllum capitatum*, *H. Fendleri*, *Onosmodium occidentale*, or *Thalictrum Fendleri*. It is believed that these results probably apply to the race recognized here, although Arthur did not inoculate *Clematis virginiana*, and in these studies *C. ligusticifolia* was not studied. Arthur considered that his material belonged in *Puccinia Agropyri*, which he later included in *Dicaeoma Clematidis*. Dietel (1892) previously had shown that the rust from *Agropyron glaucum*, similar to material from the same species described by Ellis and Everhardt under the name *Puccinia Agropyri*, had aecia on *Clematis vitalba*. To judge from the results obtained in the studies reported here, the *Elymus canadensis-Clematis ligusticifolia* and the *Agropyron glaucum-Clematis vitalba* connections are distinct races.

Aecial hosts. — This race produces aecia on *Clematis virginiana* and probably on *C. ligusticifolia*. Pycnia were developed on *Clematis orientalis* and *C. recta*.

Negative results were obtained with *Anemone cylindrica*, *A.*

virginiana, Aquilegia coerulea, Clematis Douglasii, C. Fremontii, C. Heraclaefolia, Delphinium Geyeri, Hydrophyllum capitatum, H. Fendleri, Onosmodium occidentale, Phacelia heterophylla, and *Thalictrum occidentale.*

Grass hosts. — Only *Elymus canadensis* has been found to be very susceptible. *Hordeum Gussoneanum* was moderately susceptible.

Negative results or only a few, small uredinia were obtained with *Agropyron caninum, A. cristatum, A. pseudorepens, A. repens, A. Smithii, A. tenerum, Bromus carinatus, B. ciliatus, B. polyanthus, B. tectorum, Elymus arkansanus, E. australis, E. condensatus, E. glaucus, E. virginicus, Hordeum jubatum, H. murinum, H. nodosum, H. pusillum, H. vulgare, Hystrix Hystrix, Secale cereale, Sitanion Hystrix,* and *Triticum vulgare.*

Besides the material sent to Arthur from Boulder, Colorado, this race has been studied from one collection (C 9-12418) obtained from Denver, Colorado.

15. **Puccinia rubigo-vera coloradensis,** nov. sp. f.

Aecial hosts. — This race produces pycnia and aecia on *Clematis lanuginosa* and *C. ligusticifolia.* Pycnia were obtained on *Clematis Davidiana* and *C. orientalis* also.

Negative results were obtained with *Clematis Douglasii, C. Fremontii, C. lasiantha, C. paniculata, C. recta, C. Scottii, Hydrophyllum appendiculatum,* and *Thalictrum occidentale.*

Grass hosts. — Both *Elymus canadensis* and *Elymus virginicus* are susceptible species for this race.

Negative results or only a few, small uredinia were obtained with *Agropyron caninum, A. cristatum, A. repens, A. Smithii, A. tenerum, Bromus ciliatus, Elymus arkansanus, E. australis, E. condensatus, E. glaucus, Hordeum Gussoneanum, H. jubatum, H. murinum, H. nodosum, H. pusillum, H. vulgare, Hystrix Hystrix, Secale cereale, Sitanion Hystrix,* and *Triticum vulgare.*

Two collections (C 26–22719, C 41–19020) on *Elymus canadensis* from Colorado were studied.

16. **Puccinia rubigo-vera californica,** nov. sp. f.

Aecial hosts. — This race produces aecia on *Clematis ligusticifolia.*

Negative results were obtained with *Clematis Douglasii, Delphinium Geyeri, Phacelia californica,* and *P. distans.*

Grass hosts. — *Elymus condensatus* is the only species which has proved to be susceptible.

Negative results or only a few, small uredinia were obtained with *Agropyron caninum, A. cristatum, A. repens, A. Smithii, A. tenerum, Bromus ciliatus, Elymus canadensis, E. glaucus, E. virginicus, Hordeum Gussoneanum, H. jubatum, H. nodosum, H. pusillum, H. vulgare, Hystrix Hystrix, Sitanion Hystrix,* and *Triticum vulgare.*

Two collections (C 32–3520, C 34–7220) of this race have been studied. Both were on *Elymus condensatus* from California.

17. **Puccinia rubigo-vera clematidicola,** nov. sp. f.

Aecial hosts. —Aecia of this race are produced on *Clematis ligusticifolia.* All the cultures were obtained from aecia collected in the field; a study was not made to determine the host range.

Grass hosts. — *Elymus glaucus* and *Hordeum Gussoneanum* are susceptible species.

Negative results or only a few, small uredinia were obtained with *Agropyron caninum, A. cristatum, A. intermedium, A. repens, A. Smithii, A. tenerum, Bromus carinatus, B. ciliatus, B. Kalmii, B. polyanthus, Elymus australis, E. canadensis, E. condensatus, E. robustus, E. virginicus, Hordeum jubatum, H. murinum, H. nodosum, H. pusillum, H. vulgare, Hystrix Hystrix, Secale cereale, Sitanion Hystrix,* and *Triticum vulgare.*

Three collections (C 14, C 17, C 19) of this race from Colorado (one source unknown) were studied. All were obtained from aecia, probably on *Clematis ligusticifolia.*

18. **Puccinia rubigo-vera oregonensis,** nov. sp. f.

Aecial hosts. — Both the cultures (El 28 and El 30) of this race were obtained from uredinia on *Elymus sp.* These uredinia had been developed by G. R. Hoerner at Corvallis, Oregon, from inoculations with aeciospores from aecia on *Clematis sp.*

Grass hosts. — *Elymus glaucus* and *Hordeum jubatum* were found to be favorable species.

Negative results or only a few, small uredinia were obtained with *Agropyron caninum, A. desertorum, A. repens, A. Smithii, A. tenerum, Elymus australis, E. canadensis, E. condensatus, E. robustus, E. virginicus, Hordeum Gussoneanum, H. murinum, H. nodosum, H. pusillum, H. vulgare, Hystrix Hystrix, Secale cereale, Sitanion Hystrix,* and *Triticum vulgare.*

19. **Puccinia rubigo-vera montanensis,** nov. sp. f.

Aecial hosts. — The aecial host range is not known, since this race has been studied from only one collection (C 44) of aecia, on a species of Clematis (probably *C. ligusticifolia*), from Bozeman, Montana.

Grass hosts. — *Agropyron tenerum* is the favorable host for this race. *Hordeum Gussoneanum* was moderately susceptible.

Negative results or only a few, small uredinia were obtained with *Agropyron Smithii, Elymus canadensis, E. condensatus, E. glaucus, E. virginicus, Hordeum jubatum, Hystrix Hystrix,* and *Sitanion Hystrix.*

Of the races with aecia on Clematis that have been studied in these investigations, this is the only one which has a species of Agropyron as a host.

20. **Puccinia rubigo-vera Arthuri,** nov. sp. f.

Arthur (1905, 1907, 1909) made a number of successful cultures with this race. He obtained aecia on *Clematis virginiana* from telia on *Bromus ciliatus* and *B. purgans.* He discusses his results under *Puccinia tomipara,* but states that the teliospores of his material were two-celled.

Aecial hosts. — This race produces aecia on *Clematis virginiana.*

Negative results (Arthur, *op. cit.*) were obtained with *Clematis Fremontii, C. Scottii, C. Viorna, Dirca palustris, Impatiens aurea,* and *Thalictrum dioicum.*

Grass hosts. — *Bromus ciliatus* and *B. purgans* are susceptible species.

Negative results or only a few, small uredinia were obtained with *Agropyron caninum, A. cristatum, A. intermedium, A. pseudo-repens, A. repens, A. Smithii, A. tenerum, Bromus altissimus,*

B. carinatus, B. erectus, B. hordeaceus, B. inermis, B. japonicus, B. Kalmii, B. mollis, B. polyanthus, B. pratensis, B. secalinus, B. sitchensis, B. sterilis, B. tectorum, B. villosus, B. vulgaris, Elymus australis, E. canadensis, E. condensatus, E. glaucus, E. robustus, E. virginicus, Hordeum Gussoneanum, H. jubatum, H. murinum, H. nodosum, H. pusillum, Hystrix Hystrix, Secale cereale, Sitanion Hystrix, and *Triticum vulgare.*

This race has been collected on *Bromus ciliatus* and *B. purgans* in New York, Indiana, Wisconsin, Nebraska, and Iowa (C 8–6818, C 13–25819, C 29, C 35; also Arthur, *op. cit.*).

21. Puccinia rubigo-vera bromicola, nov. sp. f.

Aecial hosts. — This race has been studied from only one collection of aecia (C 11), on a species of Clematis (probably *ligusticifolia*) obtained from Corvallis, Oregon. The range of the host species is, therefore, not known.

Grass hosts. — *Bromus carinatus, B. polyanthus,* and *B. sitchensis* are susceptible species for this race.

Negative results or only a few, small uredinia were obtained with *Agropyron caninum, A. cristatum, A. desertorum, A. intermedium, A. pseudorepens, A. repens, A. Smithii, A. tenerum, Bromus altissimus, B. ciliatus, B. erectus, B. hordeaceus, B. inermis, B. japonicus, B. Kalmii, B. pratensis, B. secalinus, B. sterilis, B. tectorum, B. villosus, B. vulgaris, Elymus arkansanus, E. australis, E. canadensis, E. condensatus, E. glaucus, E. robustus, E. virginicus, Hordeum jubatum, H. murinum, H. nodosum, H. pusillum, H. vulgare, Hystrix Hystrix, Secale cereale, Sitanion Hystrix,* and *Triticum vulgare.*

d. Other races with aecia on Clematis

The following races have been shown to have aecia on Clematis and are probably to be considered races of *Puccinia rubigo-vera.* They are listed under the hosts infected.

Clematis vitalba — Agropyron glaucum

Dietel (1892) has shown that rust on *Agropyron glaucum* in Leipzig has aecia on *Clematis vitalba.* He considered this the same

as the rust which had just previously been described by Ellis and Everhardt (1892) under the name *Puccinia Agropyri.*

Clematis ligusticifolia — Agropyron Smithii

From telia of a rust collected on *Agropyron Smithii* at Pueblo, Colorado, Arthur (1915) obtained aecia on *Clematis ligusticifolia.* He had negative results with *Anemone cylindrica, Clematis Douglasii, Delphinium sp., Hydrophyllum capitatum, H. Fendleri, Onosmodium sp.,* and *Thalictrum Fendleri.* He discusses this rust under *Puccinia Agropyri.*

Clematis pseudoflammula — Agropyron spp.

Using aeciospores from *Clematis pseudoflammula* Treboux (1912) was able to infect *Agropyron repens,* but not *Festuca elatior.* Urediniospores from *Agropyron repens* infected *Agropyron cristatum* and *A. prostratum* Eichw., but not *Andropogon Ischaemum* L., *Bromus tectorum, Diplochne serotina* Lk., or *Hordeum vulgare.* He considered that his material belonged to *Puccinia Agropyri.*

Clematis virginiana — Agropyron pseudorepens

Arthur (1908) obtained aecia on *Clematis virginiana* from telia collected on *Agropyron pseudorepens* in Colorado. Pycnia were also produced on *Viorna Scottii.*

Clematis Drummondii — Elymus virginicus

Arthur (1915) obtained aecia on *Clematis Drummondii* from telia on *Elymus virginicus* collected at Austin, Texas. Negative results were obtained with *Clematis Douglasii, C. virginiana, Aquilegia flavescens, Aq. canadensis, Thalictrum Fendleri,* and *T. dioicum.*

Clematis virginiana — Bromus Kalmii

The results obtained with collection 7218 from *Bromus Kalmii* collected at Madison, Wisconsin, indicate that there is a race on *Bromus Kalmii* with aecia on *Clematis virginiana,* since neither race *Arthuri* (20) nor *bromicola* (21) infected *Bromus Kalmii.*

Clematis spp. — Bromus Porteri

Culture 18920 from *Bromus Porteri* to *Clematis ligusticifolia* and *C. virginiana* may be a race. It may belong, however, with race *Arthuri* or *bromicola.*

Clematis ligusticifolia — Elymus triticoides

Cultures from collections 5320 and 7120 on *Elymus triticoides* may indicate a race. *Elymus triticoides,* however, was not used sufficiently in these studies to justify conclusions.

Clematis Douglasii — Hordeum jubatum

The infection of *Hordeum jubatum* from aecia on *Clematis Douglasii* (Vi 1) collected at Steamboat Springs, Colorado, indicates another race.

C. AECIA ON SPECIES OF ANEMONE AND HEPATICA

a. Results obtained from inoculations from telia on grasses to aecial hosts

Telia collected on species of Agropyron

14518. Collected on *Agropyron sp.*, Nov. 12, 1918, at Boulder, Colorado, by H. S. Jackson. This collection was used to inoculate *Anemone canadensis, A. cylindrica, Aquilegia canadensis, Aq. coerulea, Clematis virginiana, Delphinium Geyeri, Echium vulgare, Hydrophyllum sp., Myosotis palustris,* and *Phacelia sp.* Pycnia and aecia were produced on *Anemone canadensis* and *A. cylindrica* only.

25619. Telia collected on *Agropyron tenerum,* Oct. 21, 1919, at Kulm, North Dakota, by J. D. Brenkle. This was used to inoculate *Anemone cylindrica, A. quinquefolia, Anemonella thalictroides, Aquilegia coerulea, Clematis Douglasii, Delphinium Geyeri,* and *Hydrophyllum appendiculatum.* Pycnia and aecia were produced on *Anemone cylindrica* only.

Telia collected on species of Elymus

13918. Telia collected on *Elymus canadensis,* Nov. 12, 1918, at Boulder, Colorado, by H. S. Jackson. This was used to inoculate

Anemone cylindrica, Aquilegia canadensis, Aq. coerulea, Clematis Douglasii, C. orientalis, C. virginiana, and *Delphinium Geyeri.* Pycnia and aecia were produced on *Anemone cylindrica* only.

14218. Telia collected on *Elymus canadensis,* Nov. 12, 1918, at Boulder, Colorado. This was used to inoculate *Anemone cylindrica, Aquilegia coerulea, Clematis orientalis, C. virginiana, Delphinium Geyeri, Ranunculus acris,* and *Thalictrum occidentale.* Pycnia and aecia were produced on *Anemone cylindrica* only.

b. Results obtained from inoculations from aecia on Anemone to various species of grasses

The following collections were studied:

An 4. Aecia on *Anemone sp.* collected June, 1919, at Mosinee, Wisconsin, by J. J. Davis. The results of inoculations with this collection on species of grasses are given in Table XVI.

An 6. Aecia on *Anemone cylindrica* obtained by inoculation from telia on *Agropyron tenerum* (25619) from Kulm, North Dakota. The results of inoculations on species of grasses are given in Table XVI.

c. Summary of races of Puccinia rubigo-vera with aecia on species of Anemone

Three races of *Puccinia rubigo-vera* with aecia on Anemone may be distinguished. They are as follows:

22. **Puccinia rubigo-vera canadensis,** nov. sp. f.

This race has been distinguished by Fraser (1925). He believed that it should probably be considered a race of *Puccinia Clematidis,* but did not give it a name. His studies, made at Saskatoon, Saskatchewan, indicate that the host specialization is as follows:

Aecial hosts. — Aecia were collected on *Anemone cylindrica* and *A. globosa* and used to inoculate grasses.

Grass hosts. — *Agropyron dasystachum, A. Richardsonii, A. spicatum, A. tenerum,* and *Elymus canadensis* were the most susceptible species. *Elymus diversiglumis, E. virginicus,* and *Hystrix Hystrix* were moderately infected.

TABLE XVI

RESULTS OBTAINED FROM INOCULATIONS ON SPECIES OF GRASSES WITH *PUCCINIA RUBIGO-VERA* FROM AECIA ON ANEMONE (An), AQUILEGIA (Aq), DELPHINIUM (Del), AND RANUNCULUS (Ra) *

Species inoculated	An 4 †	An 6	Aq 8	Del 3	Ra 4
Agropyron caninum	−	++	−	t	..
cristatum	..	..	..	−	−
desertorum	..	..	..	−	..
intermedium	..	..	..	−	..
pseudorepens	t	t	..	..	−
repens	−	−	−	−	−
Smithii	−	−	−	t	−
tenerum	−	+++	−	+++	−
Bromus carinatus	−	..	..	−	..
ciliatus	−	−	..	..	..
japonicus	−	..	..	..	..
polyanthus	..	..	..	−	−
secalinus	..	..	..	..	−
sterilis	..	..	..	..	−
tectorum	−	..	..	..	..
Elymus australis	..	..	−	..	..
canadensis	+++	t	+++	−	−
condensatus	..	..	−	..	..
glaucus	t	++	t	..	..
robustus	..	..	+++	−	..
virginicus	+	−	−	−	−
Hordeum Gussoneanum	−	t	..	..	..
jubatum	+++	−	..	−	+++
murinum	−	−	−	..	−
nodosum	+++	..	−	..	−
pusillum	t	t	−	−	−
vulgare	−	−	..	−	−
Hystrix Hystrix	−	t	..	−	..
Puccinellia airoides	..	..	..	..	−
Secale cereale	−	−	..	−	−
Sitanion Hystrix	..	..	..	..	−
Triticum vulgare	−	−	..	−	−
Trisetum spicatum	..	..	..	..	−

* For other cultures see text.

† Accession numbers of collections. For data see text.

Negative results were obtained or slight infection occurred with *Agropyron repens, Bromus ciliatus, B. Pumpellianus, Elymus curvatus, E. innovatus, Festuca elatior, Poa compressa, P. pratensis,* and *Triticum vulgare.*

Arthur (1915) reported obtaining pycnia on *Anemone cylindrica* from telia on *Elymus canadensis* collected at Kulm, North Dakota. His material may belong here.

23. **Puccinia rubigo-vera dakotensis,** nov. sp. f.

Aecial hosts. — The aecia were obtained on *Anemone cylindrica* by inoculation from *Agropyron tenerum* (An 6–25619). The aecial host range has not been studied.

Grass hosts. — *Agropyron tenerum* is the most susceptible species. *Agropyron caninum* and *Elymus glaucus* were moderately susceptible.

Negative results or only a few, small uredinia were obtained with *Agropyron pseudorepens, A. repens, A. Smithii, Bromus ciliatus, Elymus canadensis, E. virginicus, Hordeum Gussoneanum, H. jubatum, H. pusillum, H. vulgare, Hystrix Hystrix, Secale cereale,* and *Triticum vulgare.*

Juel (1922) has obtained aecia on *Anemone hepatica* from telia on *Triticum* (*Agropyron*) *caninum.* His results may indicate a race close to *Puccinia rubigo-vera dakotensis.*

24. **Puccinia rubigo-vera** sp. f. **Hepaticae-Agropyri** (Mayor), nov. comb.

Puccinia Actaeae-Agropyri sp. f. *Hepaticae-Agropyri* Mayor. Bull. Soc. bot. suiss., 40 : 51. 1931.

Juel (1922) obtained aecia on *Actaea spicata* and *Anemone Hepatica* (*Hepatica triloba*) from telia on *Agropyron caninum.* Negative results were obtained with *Aconitum septentrionale* and *Trollius europaeus.* Mayor (1931) has considered this a race of *Puccinia Actaea-Agropyri.* This may not differ greatly from the race *dakotensis.*

25. **Puccinia rubigo-vera** sp. f. **Hepaticae-Elymi** (Mayor), nov. comb.

Puccinia Actaeae-Agropyri sp. f. *Hepaticae-Elymi* Mayor. Bull. Soc. bot. suiss., 40 : 51. 1931.

Mayor (1931) has shown that there is a race on *Elymus europaeus* which has aecia on Anemone, Helleborus, and Nigella. He obtained aecia on *Anemone Hepatica* (*Hepatica triloba*), *Helleborus foetidus*, and *Nigella damascena*. Pycnia only were obtained on *Aconitum Lycoctonum*, *Aquilegia glandulosa*, *Nigella gallica*, and *Trollius asiaticus*.

Negative results were obtained with *Anemone baldensis*, *A. coronaria*, *A. montana*, *A. nemorosa*, *A. Pulsatilla*, *A. virginiana*, *Aquilegia olympica*, *Aq. Skinneri*, *Clematis alpina*, *C. Flammula*, *C. orientalis*, *C. recta*, *C. viticella*, *Delphinium Ajacis*, *D. cashmirianum*, *D. consolida*, *D. elatum*, *D. exaltatum*, *Myosurus minimus*, *Nigella arvensis*, *Ranunculus acris*, *R. arvensis*, *R. bulbosus*, *R. platanifolius*, *Thalictrum aquilegifolium*, *T. flavum*, and *T. minus*.

From the aecia, infection was obtained on *Elymus europeus* and not on *Agropyron caninum*.

26. **Puccinia rubigo-vera anemonicola,** nov. sp. f.

Aecial hosts. — This race has been studied from one collection (An 4) of aecia on *Anemone sp.* obtained in Wisconsin.

Grass hosts. — *Elymus canadensis*, *Hordeum jubatum*, and *H. nodosum* are susceptible species.

Negative results or slight development of uredinia were obtained with *Agropyron caninum*, *A. pseudorepens*, *A. repens*, *A. Smithii*, *A. tenerum*, *Bromus carinatus*, *B. ciliatus*, *B. japonicus*, *B. tectorum*, *Elymus glaucus*, *E. virginicus*, *Hordeum Gussoneanum*, *H. murinum*, *H. pusillum*, *H. vulgare*, *Hystrix Hystrix*, *Secale cereale*, and *Triticum vulgare*.

D. AECIA ON SPECIES OF AQUILEGIA

a. Results obtained from inoculations from telia on grasses to various aecial hosts

18818. Overwintered telia collected on *Elymus sp.*, May 3, 1919, Hood River, Oregon, by H. S. Jackson. This was used to inoculate *Anemone canadensis*, *Aquilegia canadensis*, *Aq. coerulea*, *Aq. vulgaris*, *Clematis ligusticifolia*, *C. virginiana*, and *Thalictrum occidentale*, with production of pycnia and aecia on *Aquilegia canadensis*, *Aq. coerulea*, and *Aq. vulgaris*.

29119. Overwintered telia collected on *Elymus glaucus Jepsoni*, Feb. 13, 1920, at Greenville, California, by Mrs. Clemens. This was used to inoculate *Anemone cylindrica*, *Aquilegia californica*, *Aq. canadensis*, *Aq. chrysantha*, *Aq. coerulea*, *Aq. Skinneri*, *Aq. vulgaris*, *Clematis Douglasii*, *C. Fremontii*, *C. paniculata*, *C. virginiana*, *Delphinium nudicale*, *Hydrophyllum virginianum*, *Ranunculus californicus*, *Thalictrum dasycarpum*, and *T. polycarpum*. Pycnia and aecia were produced on all the species of Aquilegia.

b. Results obtained from inoculations from aecia on Aquilegia to various species of grasses

Only one culture (Aq 8) of rust from aecia on Aquilegia was studied. This was obtained from the aecia developed on *Aquilegia canadensis* by inoculating with telia from *Elymus sp.* (18818) from Hood River, Oregon. The results are given in Table XVI. This is a race with the following host specialization:

27. **Puccinia rubigo-vera Aquilegiae,** nov. sp. f.

Aecial hosts. — *Aquilegia canadensis*, *Aq. coerulea*, and *Aq. vulgaris* are susceptible species.

Negative results were obtained with *Anemone canadensis*, *Clematis ligusticifolia*, *C. virginiana*, and *Thalictrum occidentale*.

Grass hosts. — *Elymus canadensis* and *E. robustus* are susceptible species.

Negative results or only a few, small uredinia were obtained with *Agropyron caninum*, *A. repens*, *A. Smithii*, *A. tenerum*, *Elymus australis*, *E. condensatus*, *E. glaucus*, *E. virginicus*, *Hordeum murinum*, *H. nodosum*, and *H. pusillum*.

28. **Puccinia rubigo-vera** sp. f. **Agrostidis** (Plowright), nov. comb.

Puccinia Agrostidis Plowright. Gard. Chron. Third Ser., 8 : 139. 1890.

Plowright obtained aecia on *Aquilegia vulgaris* from telia on *Agrostis alba*. Inoculations from aecia produced uredinia on *Agrostis alba* and *A. vulgaris*.

Jacky, according to Klebahn (1904), obtained aecia on *Aquilegia alpina* from rust on *Agrostis alba*, and vice versa.

29. **Puccinia rubigo-vera** sp. f. **obliterata** (Arth.), nov. comb. *Puccinia obliterata* Arth. Mycologia, 1 : 250. 1909.

Arthur (1909) obtained aecia on *Aquilegia canadensis* from telia on *Agropyron biflorum* (*A. violaceum*) collected by E. W. D. Holway at Lake Louise in the Canadian Selkirks. Negative results were obtained with *Thalictrum dioicum*.

c. Other races with aecia on Aquilegia

Aquilegia spp. — Elymus glaucus Jepsoni

The results obtained with collection 29119 described under (*a*) indicate that there is probably a race with aecia on *Aquilegia californica*, *A. canadensis*, *A. chrysantha*, *A. coerulea*, *A. Skinneri*, and *A. vulgaris*, and uredinia and telia on *Elymus glaucus Jepsoni*.

E. AECIA ON SPECIES OF DELPHINIUM

a. Results obtained from inoculations from telia on grasses to aecial hosts

13718. Telia collected on *Agropyron sp.*, Nov. 12, 1918, at Boulder, Colorado, by H. S. Jackson. This collection was sown on *Aconitum Napellus*, *Actaea spicata*, *Anemone canadensis*, *A. cylindrica*, *Aquilegia coerulea*, *Clematis Douglasii*, *C. orientalis*, *C. recta*, *C. Scottii*, *C. virginiana*, *Delphinium Geyeri*, *Echium vulgare*, *Hydrophyllum appendiculatum*, *Impatiens biflora*, *Macrocalyx Nyctelea*, *Myosotis palustris*, *Phacelia tanacetifolia*, *Thalictrum aquilegifolium*, and *T. occidentale*, with the development of pycnia and aecia on *Delphinium Geyeri* only.

18220. Overwintered telia collected on *Agropyron sp.*, Feb. 27, 1921, at Golden, Colorado, by E. Bethel. This collection was sown on *Delphinium Nelsoni* and *D. Penardi*, with production of pycnia and aecia on *D. Nelsoni* only.

b. Results obtained from inoculations from aecia on Delphinium to various species of grasses

Del 3. Only one collection of aecia from Delphinium was studied on grasses. This was obtained by E. Bethel on *Delphinium sp.*, June 26, 1919, at Steamboat Springs, Colorado. The results are given in Table XVI. The host specialization of this race is apparently as follows:

30. **Puccinia rubigo-vera Delphinii,** nov. sp. f.

Aecial hosts. — Only *Delphinium Geyeri* and *D. Nelsoni* have been found to be susceptible. Probably other species of Delphinium are also hosts.

Negative results were obtained with *Aconitum Napellus, Actaea spicata, Anemone canadensis, A. cylindrica, Aquilegia coerulea, Clematis Douglasii, C. orientalis, C. recta, C. Scottii, C. virginiana, Echium vulgare, Hydrophyllum appendiculatum, Impatiens biflora, Macrocalyx Nyctelea, Myosotis palustris, Phacelia tanacetifolia, Thalictrum aquilegifolium,* and *T. occidentale.*

Grass hosts. — Only *Agropyron tenerum* was found to be a favorable host.

Negative results or only a few, small uredinia were obtained with *Agropyron caninum, A. cristatum, A. desertorum, A. intermedium, A. repens, A. Smithii, Bromus carinatus, B. polyanthus, Elymus canadensis, E. robustus, E. virginicus, Hordeum jubatum, H. pusillum, H. vulgare, Hystrix Hystrix, Secale cereale,* and *Triticum vulgare.*

For other races with aecia on Delphinium consult Section G ("Aecia on species of Actaea").

F. AECIA ON SPECIES OF RANUNCULUS

a. Results obtained from inoculations from telia on species of grasses to aecial hosts

Telia collected on species of Puccinellia

11518. Telia collected on *Puccinellia airoides* (Nutt.) Wats., Nov., 1918, at Denver, Colorado, by H. S. Jackson. This col-

lection was sown on *Aquilegia canadensis, Clematis ligusticifolia, C. orientalis, C. virginiana, Ranunculus aconitifolius, R. Cymbalaria, R. repens,* and *Thalictrum dioicum,* with production of pycnia and aecia on *R. Cymbalaria* only.

11419. Telia collected on *Puccinellia airoides,* July 18, 1919, at Denver, Colorado, by E. Bethel and G. H. Coons. This collection was used to inoculate *Ranunculus abortivus, R. acris, R. californicus, R. Cymbalaria, R. repens,* and *R. sceleratus,* with production of pycnia and aecia on *R. Cymbalaria* only.

16220. Telia collected on *Puccinellia airoides,* Oct. 24, 1920, at Denver, Colorado, by E. Bethel. This collection was used to inoculate *Ranunculus abortivus, R. acris, R. Cymbalaria, R. lanuginosus,* and *R. sceleratus,* with production of pycnia and aecia on *R. cymbalaria* only.

Telia collected on species of Poa

1520. Overwintered telia collected on *Poa sp.,* May 14, 1920, at Atascadera, California, by E. Bethel. This collection was used to inoculate *Ranunculus abortivus, R. californicus, R. Cymbalaria,* and *R. sceleratus,* with development of pycnia and aecia on *R. californicus* only.

b. Results obtained from inoculations from aecia on Ranunculns to various species of grasses

The following collections were studied:

Ra 3. Aecia from *Ranunculus Cymbalaria* obtained by inoculation from *Puccinellia airoides* (11518) from Denver, Colorado. This was sown on *Agropyron repens, Bromus Kalmii, B. sitchensis, Elymus virginicus, Hordeum jubatum, H. murinum, Puccinellia airoides,* and *Sitanion Hystrix,* with production of uredinia on *Puccinellia airoides* only.

Ra 4. Aecia collected on *Ranunculus Cymbalaria,* June 26, 1919, at Steamboat Springs, Colorado, by E. Bethel, were used to inoculate a series of species of grasses, with the results given in Table XVI.

Ra 7. Aecia developed on *Ranunculus Cymbalaria* from inocu-

lations with telia from *Puccinellia airoides* (11419) from Denver, Colorado, were used to inoculate *Aira flexuosa, Alopecurus pratensis, Avena fatua, Briza media, Bromus carinatus, B. tectorum, B. villosus, Dactylis glomerata, Festuca octoflora* Walt., *Glyceria nervata* (Willd.) Trin., *Hordeum jubatum, H. vulgare, Koeleria gracilis, Poa fertilis, P. lucida* Vasey, *P. palustris, P. pratensis* L., *P. Sandbergii, P. triflora* Gilib., *P. trivialis* L., *Puccinellia airoides, Secale cereale, Sphenopholis obtusata* (Michx.) Scribn., and *Triticum vulgare,* with production of uredinia on *Puccinellia airoides* only.

Ra 10. Aecia developed on *Ranunculus Cymbalaria* from inoculations with telia from *Puccinellia airoides* (16220) from Denver, Colorado, were used to inoculate *Aira flexuosa, Alopecurus pratensis, Arrhenatherum elatius, Avena barbata, Av. fatua, Dactylis glomerata, Festuca ovina, F. rubra, Notholcus lanatus, Poa palustris, P. pratensis, P. trivialis, Puccinellia airoides, Sphenopholis obtusata,* and *S. pallens* (Spreng.) Scribn., with production of uredinia on *Puccinellia airoides* only.

c. Races of Puccinia rubigo-vera with aecia on Ranunculus

31. **Puccinia rubigo-vera Puccinelliae,** nov. sp. f.

Arthur (1909) demonstrated that telia from *Puccinellia airoides,* collected by E. Bethel at Aravada, Colorado, were connected with aecia on *Ranunculus Cymbalaria.* The results of these studies (Ra 3–11518, Ra 7–11419, Ra 10–16220) indicate that it is a distinct race, with the following host specialization.

Aecial host. — *Ranunculus Cymbalaria* was the only species on which aecia were produced.

Negative results were obtained with *Aquilegia canadensis, Clematis ligusticifolia, C. orientalis, C. virginiana, Ranunculus abortivus, R. aconitifolius, R. acris, R. californicus, R. lanuginosus, R. repens, R. sceleratus,* and *Thalictrum dioicum.*

Grass host. — Only *Puccinellia airoides* was susceptible.

Negative results were obtained with *Agropyron repens, Aira flexuosa, Alopecurus pratensis, Arrhenatherum elatius, Avena barbata, Av. fatua, Briza media, Bromus carinatus, B. Kalmii, B.*

sitchensis, B. tectorum, B. villosus, Dactylis glomerata, Elymus virginicus, Festuca octoflora, F. ovina, F. rubra, Glyceria nervata, Hordeum jubatum, H. murinum, H. vulgare, Koeleria gracilis, Notholcus lanatus, Poa fertilis, P. lucida, P. palustris, P. pratensis, P. Sandbergii, P. triflora, P. trivialis, Secale cereale, Sphenopholis obtusata, S. pallens, and *Triticum vulgare.*

There is probably also a race having aecia on *Ranunculus Cymbalaria* and uredinia and telia on species of Poa. Arthur (1909) states that J. M. Bates observed in Nebraska rusted species of Poa (*Puccinia cinerea* Arth.) growing in close proximity to *Ranunculus Cymbalaria* with aecia.

The results with collection 1520 indicate that there may be a race in California having uredinia and telia on species of Poa and aecia on *Ranunculus californicus.*

32. **Puccinia rubigo-vera alpina,** nov. sp. f.

Aecial host. — Only one collection (Ra 4) of this race was studied from aecia on *Ranunculus Cymbalaria,* obtained at Steamboat Springs, Colorado. It probably is restricted to this species.

Grass host. — Only *Hordeum jubatum* was susceptible.

Negative results were obtained with *Agropyron cristatum, A. pseudorepens, A. repens, A. Smithii, A. tenerum, Bromus polyanthus, B. secalinus, Elymus canadensis, E. virginicus, Hordeum murinum, H. nodosum, H. pusillum, H. vulgare, Puccinellia airoides, Secale cereale, Sitanion Hystrix, Triticum vulgare,* and *Trisetum spicatum.*

33. **Puccinia rubigo-vera** sp. f. **perplexans** (Plowr.), nov. comb.
Puccinia perplexans Plowr. Quart. Journ. Microsc. Sci., 25 : 164. 1885.

Plowright (1885) demonstrated that telia on *Alopecurus pratensis* and *Avena elatior* were connected with aecia on *Ranunculus acris* in England. Aeciospores sown on *Alopecurus (pratensis), Avena elatior, Dactylis glomerata, Lolium perenne, Poa compressa, P. nemoralis, P. pratensis,* and *P. trivialis* gave infection on *Alopecurus pratensis* and *Avena elatior* only.

In Germany Dietel (1889) obtained uredinia on *Alopecurus*

pratensis from aecia on *Ranunculus acris*. Klebahn (1902) had similar results. In Nova Scotia Fraser (1912) obtained aecia on *Ranunculus acris* from telia on *Alopecurus pratensis*. In Russia Tranzschel (1914) reported the infection of *Ranunculus acris* with telia from *Alopecurus brachystachyus* M. B.

G. AECIA ON SPECIES OF ACTAEA

No cultures from aecia on species of Actaea were studied in these investigations. In the literature, however, several connections have been recorded indicating several races.

34. **Puccinia rubigo-vera** sp. f. **Actaeae-Agropyri** (Ed. Fischer), nov. comb.

Puccinia Actaeae-Agropyri Ed. Fischer. Ber. schweiz. bot. Gesell., 11 : 8. 1901.

Puccinia Actaeae-Agropyri sp. f. *typica* Mayor. Bull. Soc. bot. suiss., 40 : 51. 1931.

Fischer (1901) inoculated *Actaea spicata, Thalictrum aquilegifolium,* and *T. minus* from telia on *Agropyron caninum,* obtaining aecia on *Actaea spicata.* From the aecia he was able to infect *Agropyron caninum,* but not *Agropyron repens* or *Poa nemoralis.* Mayor (1920) showed that this race has a rather wide host range for the aecia, resembling the next race, *Actaeae-Elymi.* From aecia on *Actaea spicata* he obtained infection on *Agropyron caninum,* but not on *Agropyron repens, Elymus europaeus,* or *Festuca violacea.* From telia on *Agropyron caninum* he obtained aecia not only on *Actaea spicata,* but also on *Aconitum Lycoctonum, A. paniculatum, Delphinium Consolida, Helleborus foetidus,* and *Nigella damascena.*

35. **Puccinia rubigo-vera** sp. f. **Actaeae-Elymi** (Mayor), nov. comb.

Puccinia Actaeae-Elymi Mayor. Ann. Mycol., 9 : 361. 1911.

Puccinia Actaeae-Agropyri sp. f. *Actaeae-Elymi* E. Mayor. Bull. Soc. bot. suiss., 40 : 51. 1931.

Mayor (1911, 1920, 1931) has shown that this race has aecia on *Aconitum Anthora, A. Lycoctonum, A. Napellus, A. paniculatum,*

A. pyrenaicum, A. Stoerkianum, A. variegatum, Actaea cimicifuga, A. spicata, Adonis aestivalis, Ad. annua, Aquilegia glandulosa, Delphinium Ajacis, D. cashmirianum, D. Consolida, D. dictyocarpum, D. elatum, D. exaltatum, D. nudicaule, D. Staphysagria, Eranthis hiemalis, Helleborus caucasicus, H. foetidus, H. niger, H. viridis, Leptopyrum fumarioides, Nigella arvensis, N. damascena, and *N. gallica.* Pycnia only were obtained on *Aquilegia alpina, Aq. chrysantha, Aq. coerulea, Aq. fragrans, Aq. nivea, Aq. olympica, Aq. sibirica, Aq. Skinneri, Aq. vulgaris, Isopyrum thalictroides,* and *Trollius asiaticus.*

Negative results were obtained with *Anemone baldensis, A. coronaria, A. nemorosa, A. Pulsatilla, A. ranunculoides, A. virginiana, Caltha palustris, Clematis alpina, C. recta, C. orientalis, Hepatica triloba* (*Anemone Hepatica*), *Myosurus minimus, Paeonia* aff. *officinalis, P. montana, Ranunculus abortivus, R. acris, R. arvensis, R. bulbosus, R. Ficaria, R. platanifolius, R. repens, R. silvaticus, Thalictrum alpinum, T. aquilegifolium, T. flavum, T. foetidum, T. minus, Trollius europaeus,* and *T. Ledebourii.*

Of the species of grasses studied only *Elymus europaeus* proved to be susceptible. Negative results were obtained with *Agropyron repens, A. caninum, Festuca rubra genuina, F. rubra commutata,* and *F. rubra violacea.*

This race is of special interest on account of the wide range of aecial hosts, twenty-nine species of nine genera. Mayor found that it was morphologically very similar to *Actaeae-Agropyri,* but separated sharply by its grass host.

36. **Puccinia rubigo-vera septentrionalis,** nov. sp. f.

Fraser (1920, 1925) inoculated *Actaea rubra* with telia from *Hystrix patula* (*Hystrix*), collected at Ste Anne de Bellevue, Province of Quebec, and obtained aecia. Inoculations from aecia on *Actaea rubra* to *Agropyron repens, A. Richardsonii, Bromus ciliatus, Elymus canadensis, E. virginicus, Hordeum jubatum,* and *Hystrix Hystrix* gave abundant infection on *Elymus canadensis, E. virginicus,* and *Hystrix Hystrix;* slight infection was obtained on *Hordeum jubatum.* In one instance heavy infection was

obtained on *Agropyron Richardsonii* and in another there were no results.

Negative results were obtained with *Agropyron repens* and *Bromus ciliatus*. Abundant aecia were found on *Actaea alba* in the field. Fraser considered this a race of *Puccinia Clematidis*, but gave it no designation.

H. AECIA ON SPECIES OF ACONITUM

The following race occurs with aecia on Aconitum:

37. **Puccinia rubigo-vera** sp. f. **Aconiti-rubrae** (Lüdi), nov. comb.

Puccinia Aconiti-rubrae Lüdi. Mitteil. Naturforsch. Gesell. Bern, 1918, pp. 200–211.

According to Sydow (1924), Lüdi has shown that rust on *Festuca rubra commutata* and *violacea* produce aecia on *Aconitum Napellus, A. paniculatum, A. variegatum*, and *A. Stoerkianum*, but not on *A. Lycoctonum, A. Anthora, Helleborus foetidus*, or *H. viridis*. From aecia the rust was produced on *Festuca rubra commutata* and *F. rubra violacea*, but not on *F. rubra genuina, Elymus europaeus*, or *Poa spp.*

The aecial hosts of this race are apparently restricted to the blue-flowered species of Aconitum.

Sydow (1924) states that Lagerheim has observed association of aecia on *Aconitum septentrionalis* with telia on *Agropyron* (*Triticum*) *caninum* (*Puccinia subalpina* Lagerh.), and that Liro has observed the same connection (*Puccinia aecidii-mamallati* Liro).

I. AECIA ON SPECIES OF TROLLIUS

According to the literature, one race with aecia on Trollius occurs:

38. **Puccinia rubigo-vera** sp. f. **Dietrichiana** (Tranzschel), nov. comb.

Puccinia Dietrichiana Tranzschel. Ann. Mycol., 5 : 418. 1907.

Tranzschel (1907) has shown that in Russia telia on *Agropyron* (*Triticum*) *caninum* produced aecia on *Trollius europeus* L. The aeciospores developed rust on *Agropyron caninum*, but not on *Poa nemoralis*.

J. AECIA ON SPECIES OF ANCHUSA

a. Results obtained from inoculations from telia on grasses to aecial hosts

The results of these studies have been previously reported (Mains and Jackson, 1924). From telia on rye, *Secale cereale*, aecia were produced on *Anchusa officinalis* and *A. capensis* Thunb. A few pycnia were obtained on one plant of *Nonnea rosea* Link. Negative results were obtained with *Cerinthe minor*, *C. major* L., *C. alpina* Kit., *Lappula echinata* Gilib., *Myosotis palustris* Hill, *M. arvensis* (L.) Hill, *M. alpestris* F. W. Schmidt, *M. virginica* (L.) BSP., *Nonnea lutea* DC., *Symphytum asperum* Lepechin, and *Pulmonaria officinalis* L.

De Bary (1867) was the first to prove this connection. From teliospores on rye he produced aecia on *Anchusa arvensis* and *A. officinalis*. He had negative results with *Berberis vulgaris*, *Ranunculus acris*, *R. bulbosus*, *Rhamnus frangula*, *R. cathartica*, *Taraxacum officinale*, and *Urtica dioica*. Studies by Nielson (1877), Plowright (1889), Eriksson (1899), Klebahn (1904), and Arthur (1909, 1916) have given similar results.

b. Results obtained by inoculations from aecia on Anchusa to various species of grasses

Aecia obtained in the greenhouse at Lafayette, Indiana, in 1919, as a result of inoculations from telia on rye were sown on a number of species of grasses. Uredinia were produced abundantly on rye, *Secale cereale*. As has been stated elsewhere (Mains and Leighty, 1923; Mains, 1926), practically all the so-called varieties of rye contain both susceptible and more or less resistant individuals. Negative results were obtained with *Agropyron caninum*, *A. repens*, *A. Smithii*, *A. tenerum*, *Alopecurus geniculatus*, *Avena barbata*, *A. fatua*, *Bromus altissimus*, *B. ciliatus*, *B. commutatus*,

B. hordeaceus, B. inermis, B. japonicus, B. mollis, B. polyanthus, B. pratensis, B. pumpellianus, B. rubens, B. secalinus, B. sitchensis, B. sterilis, B. tectorum, B. villosus, B. vulgaris, Elymus canadensis, E. virginicus, Glyceria nervata, Hordeum Gussoneanum, H. murinum, H. pusillum, Hystrix Hystrix, Triticum dicoccum, T. durum, T. polonicum, and *T. spelta.*

c. Results obtained by inoculations from uredinia on rye to various species of grasses

The following collections were studied:

Ry 2. Collected on rye, May 5, 1918, at New Madrid, Missouri, by A. C. Martin. This produced uredinia on rye only; some individuals showed resistance. Negative results were obtained with *Agropyron intermedium, A. tenerum, Bromus altissimus, B. carinatus, B. ciliatus, B. erectus, B. hordeaceus, B. inermis, B. japonicus, B. Kalmii, B. polyanthus, B. secalinus, B. sitchensis, B. sterilis, B. tectorum, B. villosus, Elymus robustus, Hordeum pusillum, H. vulgare, Hystrix Hystrix, Puccinellia airoides, Sitanion Hystrix,* and *Triticum vulgare.*

Ry 8. Collected on rye in 1918 at St. Paul, Minnesota, by H. S. Jackson. This produced uredinia on rye only; some individuals showed resistance. Negative results were obtained with *Agropyron intermedium, A. tenerum, Elymus robustus, Hordeum pusillum, H. vulgare, Hystrix Hystrix, Puccinellia airoides, Sitanion Hystrix,* and *Triticum vulgare.*

Ry 9. Collected on rye, Nov. 4, 1918, at Fargo, North Dakota, by H. S. Jackson. This produced uredinia on rye only; some individuals showed some resistance. Negative results were obtained with *Agropyron caninum, A. repens, A. Smithii, A. tenerum, Alopecurus geniculatus, Al. pratensis, Bromus carinatus, B. japonicus, B. Kalmii, B. secalinus, B. sitchensis, B. sterilis, B. tectorum, B. villosus, B. vulgaris, Elymus australis, E. canadensis, E. robustus, Festuca elatior, F. rubra, Hordeum jubatum, H. murinum, H. pusillum, Hystrix Hystrix, Panicularia borealis, Puccinellia airoides,* and *Sitanion Hystrix.*

Ry 11. Collected on rye, Nov. 30, 1918, at Belleville, Illinois,

by L. S. Cheney. This produced uredinia on rye only; some individuals showed resistance. Negative results were obtained with *Agropyron caninum, A. cristatum, A. desertorum, A. intermedium, A. pseudorepens, A. repens, A. Smithii, A. tenerum, Alopecurus geniculatus, Al. pratensis, Bromus altissimus, B. carinatus, B. ciliatus, B. inermis, B. japonicus, B. Kalmii, B. pratensis, B. secalinus, B. sitchensis, B. sterilis, B. tectorum, B. villosus, B. vulgaris, Elymus arkansanus, E. australis, E. canadensis, E. condensatus, E. glaucus, E. robustus, E. virginicus, Festuca ovina, F. pratensis, F. rubra, F. tenuifolia, Hordeum jubatum, H. murinum, H. pusillum, H. vulgare, Hystrix Hystrix, Sitanion Hystrix*, and *Triticum vulgare.*

Ry 12. Collected on rye, Oct. 25, 1918, at Lafayette, Indiana, by the writer. This produced uredinia on rye only; some individuals showed resistance. Negative results were obtained with *Agropyron intermedium, A. tenerum, Elymus robustus, Hordeum pusillum, H. vulgare, Hystrix Hystrix, Puccinellia airoides, Sitanion Hystrix*, and *Triticum vulgare.*

Ry 20. Collected on rye, Sept. 8, 1921, at Lafayette, Indiana, by the writer. This produced uredinia on rye, *Secale cereale* and *Secale montanum.* The varieties Petkus, Star, Rosen, Wis. No. 2, Mammoth Winter, and Abruzzes were inoculated and each showed a few resistant individuals. From a total of 346 plants inoculated 303 were susceptible and 43 were more or less resistant. Similar results were obtained with *Secale montanum.* A majority of the plants were susceptible. A few individuals, however, were found showing more or less resistance, types 2, 1, and 0.

Negative results were obtained with *Agropyron caninum, A. cristatum, A. repens, A. tenerum, Elymus arenarius, E. canadensis, E. condensatus, E. giganteus, E. glaucus, E. sibericus, E. striatus, E. triticoides, E. virginicus, Hordeum boreale, H. jubatum, H. nodosum, H. pusillum*, and *Hystrix Hystrix.* This culture was also sown on eight lines derived from wheat-rye crosses received from Dr. C. E. Leighty. These were several generations removed from the cross and mostly resembled wheat. Over fifty plants of each were inoculated, but none showed any signs of rust.

Eriksson and Henning (1894) found that aeciospores from aecia

produced on *Anchusa arvensis* from telia on rye developed uredinia on rye only, whereas inoculations on wheat, oats, and barley gave negative results. They therefore recognized the leaf rust of rye as a specialized form, *Secalis*, of *Puccinia dispersa*. Eriksson (1894) inoculated *Triticum vulgare* and *Secale cereale* with rust from *Secale cereale* and obtained infection on the latter only. Eriksson later (1899) inoculated *Agropyron repens* (*Triticum repens*), *Bromus arvensis*, *Holcus lanatus*, *Secale cereale*, and *Triticum vulgare* with aeciospores from *Anchusa arvensis* which had been produced from telia on rye. Only *Secale cereale* produced uredinia. Likewise inoculations with urediniospores from rye on *Agropyron repens*, *Bromus arvensis*, *B. mollis*, *Holcus lanatus*, *Secale cereale*, *Trisetum flavescens*, and *Triticum vulgare* produced uredinia on the last only. Carleton (1899) inoculated *Anthoxanthum odoratum*, *Agropyron caninum*, *A. repens*, *A. tenerum*, *A. villosum*, *Avena sativa*, *Dactylis glomerata*, *Elymus canadensis*, *E. condensatus*, *E. virginicus*, *Festuca gigantea*, *Hordeum murinum*, *H. vulgare*, *Koeleria cristata*, *Poa nemoralis*, *P. pratensis*, *Secale cereale*, *S. montanum*, *Sporobolus asper*, *Triticum vulgare*, and *Zea mays* with uredinia from rye and obtained uredinia on *Secale cereale* and *S. montanum* only.

This race of *Puccinia rubigo-vera* may be designated as follows:

39. **Puccinia rubigo-vera** sp. f. **Secalis** (Erikss. & Henn.) Carleton. U. S. Dept. Agric., Div. Veg. Phy. Path., Bull. 16 : 42. 1899.

Puccinia dispersa Secalis Erikss. & Henn. Zeitschr. Pflanzenkrank., 4 : 259. 1894.

Puccinia dispersa Erikss. Ann. Sci. Nat., Eighth Ser., 9 : 268. 1899.

Puccinia secalina Grove. The British Rust Fungi, p. 261. 1913.

Aecial hosts. — The results of the studies of De Bary (1867), Nielson (1877), Plowright (1889), Eriksson (1899), Klebahn (1904) Arthur (1909, 1916), and Mains and Jackson (1924) have shown that this race produces its aecia on *Anchusa arvensis*, *A. capensis*, and *A. officinalis*. Pycnia have been obtained on *Nonnea rosea*.

Negative results have been obtained with *Berberis vulgaris, Cerinthe minor, C. major, C. alpina, Lappula echinata, Myosotis alpestris, M. arvensis, M. palustris, M. virginica, Nonnea lutea, Pulmonaria officinalis, Ranunculus acris, R. bulbosus, Symphytum asperum, Taraxacum officinale,* and *Urtica dioica.*

Grass hosts. — Only *Secale cereale* and *S. montanum* have been found to be susceptible hosts.

Negative results have been obtained with *Agropyron caninum, A. cristatum, A. desertorum, A. intermedium, A. pseudorepens, A. repens, A. Smithii, A tenerum, A. villosum, Alopecurus geniculatus, Al. pratensis, Anthoxanthum odoratum, Avena barbata, Av. fatua, Av. sativa, Bromus altissimus, B. arvensis, B. carinatus, B. ciliatus, B. commutatus, B. erectus, B. hordeaceus, B. inermis, B. japonicus, B. Kalmii, B. mollis, B. polyanthus, B. pratensis, B. Pumpellianus, B. rubens, B. secalinus, B. sitchensis, B. sterilis, B. tectorum, B. villosus, B. vulgaris, Dactylis glomerata, Elymus arenarius, E. arkansanus, E. australis, E. canadensis, E. condensatus, E. giganteus, E. glaucus, E. robustus, E. sibiricus, E. striatus, E. triticoides, E. virginicus, Festuca elatior, F. gigantea, F. ovina, F. pratensis, F. rubra, F. tenuifolia, Glyceria nervata, Holcus lanatus, Hordeum boreale, H. Gussoneanum, H. jubatum, H. murinum, H. nodosum, H. pusillum, H. vulgare, Hystrix Hystrix, Koeleria cristata, Melica altissima, Panicularia borealis, Phleum pratense, Poa pratensis, P. triflora, Puccinellia airoides, Sitanion Hystrix, Sporobolus asper, Trisetum flavescens, Triticum dicoccum, T. durum, T. polonicum, T. Spelta, T. vulgare,* and *Zea mays.*

There is some evidence (Mains, 1926) that this race may be still further divided into physiologic forms by the use of selections of rye.

K. AECIA ON SPECIES OF ONOSMODIUM AND MACROCALYX

Aecia collected by E. Bethel on *Onosmodium occidentale* at Boulder, Colorado, June 21, 1919, were used (On 1) to inoculate *Agropyron caninum, A. pseudorepens, A. repens, A. Smithii, A. tenerum, Elymus australis, E. canadensis, E. condensatus, E. glaucus, E. robustus, E. virginicus, Hordeum Gussoneanum,*

H. jubatum, H. murinum, H. nodosum, H. pusillum, H. vulgare, Hystrix Hystrix, Secale cereale, Sitanion Hystrix, and *Triticum vulgare. Agropyron Smithii* was very susceptible, and *Elymus condensatus* was moderately so.

Telia (19219) produced on *Agropyron Smithii* in the foregoing study were used to inoculate *Anchusa officinalis, Cerinthe minor, Cynoglossum officinale, Hydrophyllum appendiculatum, H. virginianum, Macrocalyx Nyctelea, Mertensia virginica, Myosotis sempervirens, Onosmodium occidentale, Phacelia californica,* and *P. Purshii.* Pycnia and aecia developed on *Macrocalyx Nyctelea* and *Onosmodium occidentale.* The aecia produced on *Macrocalyx Nyctelea* (Mac 2) were used to inoculate *Agropyron caninum, A. desertorum, A. Smithii, A. tenerum, Elymus canadensis, E. glaucus, E. striatus, E. virginicus, Hordeum jubatum, H. nodosum, H. vulgare,* and *Hystrix Hystrix.* Uredinia were developed abundantly on *Agropyron Smithii* only.

This race, therefore, has the following host specialization:

40. Puccinia rubigo-vera Onosmodii, nov. sp. f.

Aecial hosts. — *Macrocalyx Nyctelea* and *Onosmodium occidentale* are aecial hosts.

Negative results were obtained with *Anchusa officinalis, Cerinthe minor, Cynoglossum officinale, Hydrophyllum appendiculatum, H. virginianum, Mertensia virginica, Myosotis sempervirens, Phacelia californica,* and *P. Purshii.*

Grass hosts. — *Agropyron Smithii* was the most susceptible species studied. *Elymus condensatus* was moderately susceptible.

Negative results or only a few, small uredinia were obtained with *Agropyron caninum, A. desertorum, A. pseudorepens, A. repens, A. tenerum, Elymus canadensis, E. glaucus, E. robustus, E. striatus, E. virginicus, Hordeum Gussoneanum, H. jubatum, H. murinum, H. nodosum, H. pusillum, H. vulgare, Hystrix Hystrix, Secale cereale, Sitanion Hystrix,* and *Triticum vulgare.*

This race is of special interest since one aecial host, *Macrocalyx Nyctelea,* is in the Hydrophyllaceae and the other, *Onosmodium occidentale,* is in the Boraginaceae.

L. AECIA ON SPECIES OF SYMPHYTUM AND PULMONARIA

F. Müller (1901) has shown that there is a rust of Bromus with aecia on *Pulmonaria montana* and *Symphytum officinale*, which he named *Puccinia Symphyti-Bromorum*. This is apparently a distinct race of *Puccinia rubigo-vera* and may be designated as follows:

41. **Puccinia rubigo-vera** sp. f. **Symphyti-Bromorum** (F. Müller) nov. comb.
Puccinia Symphyti-Bromorum F. Müller. Bot. Centralbl., Beihefte 10 : 201. 1901.

Aecial hosts. — *Pulmonaria montana* and *Symphytum officinale* were found to be susceptible species. A weak development of pycnia was obtained on *Anchusa officinalis* and *Nonnea rosea*.

Negative results were obtained with *Anchusa arvensis, Cerinthe alpina, Cynoglossum officinale, Echium rubrum, E. vulgare, Myosotis alpestris, M. arvensis, M. silvatica, Omphalodes verna, Pulmonaria officinalis*, and *Symphytum asperrimum*.

Grass hosts. — *Bromus arvensis, B. brachystachys, B. erectus, B. inermis, B. macrostachys, B. mollis*, and *B. secalinus* were susceptible species.

Negative results were obtained with *Arrhenatherum elatius, Alopecurus pratensis, Avena sativa, Bromus brizaeformis, Festuca elatior, Holcus lanatus, Secale cereale, Trisetum flavescens*, and *Triticum vulgare*.

M. AECIA ON LITHOSPERMUM AND MYOSOTIS

Treboux (1912) has connected aecia on species of Lithospermum and Myosotis with rust on species of Bromus which he considered under *Puccinia bromina*. This probably represents a race which may be designated as follows:

42. **Puccinia rubigo-vera Lithospermi,** nov. sp. f.

Treboux sowed aeciospores from aecia on *Lithospermum arvense* on *Bromus tectorum* and *Bromus squarrosus* with positive results. Aeciospores from aecia on *Myosotis silvatica* were sown on *Bromus*

tectorum with positive results. Urediniospores from *Bromus tectorum* were sown on *Bromus inermis, B. squarrosus,* and *B. tectorum,* producing infection on all three. It is not clear whether the last culture was made with uredinia connected with aecia on both hosts and whether both aecial hosts belong to the same race.

N. RACES ON BROMUS WITH AECIA UNKNOWN

Eriksson (1894) found that there was a race restricted to species of Bromus which he first considered a specialized form *Bromi* of *Puccinia dispersa* and later (1899) separated as a species, *Puccinia bromina* Erikss. He was not able to connect this with aecia. It is placed here for convenience and is distinguished as follows:

43. **Puccinia rubigo-vera** sp. f. **Bromi** (Erikss.), nov. comb.
Puccinia dispersa sp. f. *Bromi* Erikss. Deut. Bot. Gesell., 12 : 316. 1894.
Puccinia bromina Erikss. Ann. Sci. Nat., Eighth Ser., 9 : 271. 1899.

Aecial hosts. — Unknown.

Negative results were obtained by Eriksson with *Anchusa arvensis, A. officinalis, Myosotis alpestris, Nonnea rosea, Pulmonaria officinalis,* and *Symphytum asperrimum.*

Grass hosts. — *Bromus arduennensis, B. arvensis, B. asper, B. brizaeformis, B. macrostachys, B. mollis, B. patulus, B. racemosus, B. secalinus, B. squarrosus, B. sterilis,* and *B. tectorum* were susceptible species.

Negative results were obtained with *Agropyron repens, Avena sativa, Bromus erectus, B. inermis, Holcus lanatus, Hordeum vulgare, Secale cereale,* and *Triticum vulgare.*

Bromus brizaeformis is susceptible to this race and resistant to *Symphyti-Bromorum,* whereas the reverse is true for *Bromus erectus* and *B. inermis.*

Ward (1902*a*, 1902*b*, 1903) and Freeman (1902) made extensive studies with *Puccinia rubigo-vera* from species of Bromus, which they considered under the name *Puccinia dispersa.* They did not connect the races with which they were working with aecia.

Their results, which are somewhat difficult to interpret, will, however, be briefly considered here. They indicate the number of plants inoculated by the denominator of a fraction and the number successfully infected by the numerator. Thus the results of sowing rust from *Bromus sterilis* upon *B. sterilis* are given as $\frac{1}{1}\frac{2}{4}\frac{6}{6}$. The question arises whether this signifies resistant individuals in *Bromus sterilis*, or faulty technic.

Their results, however, indicate that a number of races occur in the rust of Bromus. These may be distinguished as follows:

44. **Puccinia rubigo-vera Stenobromi,** nov. sp. f.

Ward (1903) studied rust obtained from *Bromus sterilis.* To judge from the data given, *Bromus purpurascens, B. rubens,* and *B. sterilis* are the most favorable species. *Bromus arduennensis* var. *villosus, B. Gussonii, B. madritensis,* and *B. pendulinus* were moderately susceptible. *Bromus Krausii, B. maximus, B. molliformis, B. mollis,* and *B. vestitus* were apparently more or less resistant.

Negative results were obtained with *Bromus adoensis, B. angustifolius, B. arduennensis, B. arvensis, B. asper, B. Biebersteini, B. breviaristatus, B. brizaeformis, B. carinatus, B. ciliaris, B. ciliatus, B. commutatus, B. condensatus, B. erectus, B. fibrosus, B. grossus, B. inermis, B. interruptus, B. Kalmii, B. laxus, B. macrostachys, B. multiflorus, B. parviflorus, B. patulus, B. pitensis, B. Pumpellianus, B. pungens, B. racemosus, B. rigidus, B. Schraderi, B. secalinus, B. segetum, B. squarrosus, B. squarrosus villosus, B. tectorum, B. unioloides, B. valdivianus, B. velutinus,* and *B. virens.*

45. **Puccinia rubigo-vera arvensis,** nov. sp. f.

This race was obtained from *Bromus arvensis. Bromus arvensis, B. brachystachys, B. macrostachys, B. patulus, B. pendulinus, B. purpurascens, B. rubens, B. secalinus,* and *B. squarrosus* were the most favorable species. *Bromus brizaeformis, B. mollis, B. rigidus,* and *B. velutinus* apparently were moderately susceptible. *Bromus hordeaceus* and *B. interruptus* were apparently more or less resistant.

Negative results were obtained with *Bromus asper, B. carinatus,*

B. commutatus, *B. erectus*, *B. Gussonii*, *B. laxus*, *B. madritensis*, *B. propendens*, *B. racemosus*, *B. segetum*, *B. sterilis*, *B. tectorum*, *B. valdivianus*, and *B. virens*.

46. **Puccinia rubigo-vera Zeobromi**, nov. sp. f.

This race was obtained from *Bromus mollis*. *Bromus adoensis*, *B. arduennensis*, *B. arduennensis villosus*, *B. brachystachys*, *B. hordeaceus*, *B. Krausii*, *B. mollis*, *B. squarrosus*, *B. squarrosus villosus*, and *B. vestitus* were the most favorable species. *Bromus brizaeformis*, *B. grossus*, *B. interruptus*, *B. multiflorus*, *B. pendulinus*, *B. secalinus*, and *B. velutinus* were apparently moderately susceptible. *Bromus arvensis*, *B. asper*, *B. commutatus*, *B. erectus*, *B. Gussonii*, *B. macrostachys*, *B. maximus*, *B. molliformis*, *B. patulus*, *B. racemosus*, and *B. sterilis* were apparently more or less resistant.

Negative results were obtained with *Bromus angustifolius*, *B. Biebersteini*, *B. breviaristatus*, *B. canadensis*, *B. carinatus*, *B. ciliaris*, *B. ciliatus*, *B. condensatus*, *B. fibrosus*, *B. inermis*, *B. Kalmii*, *B. laxus*, *B. madritensis*, *B. parviflorus*, *B. pitensis*, *B. Pumpellianus*, *B. purgans*, *B. Schraderi*, *B. segetum*, *B. tectorum*, *B. unioloides*, *B. valdivianus*, and *B. virens*.

47. **Puccinia rubigo-vera Wardii**, nov. sp. f.

This race was obtained from *Bromus brizaeformis*. *Bromus arvensis*, *B. brachystachys*, *B. hordeaceus*, *B. macrostachys*, *B. madritensis*, *B. mollis*, *B. patulus*, *B. pendulinus*, *B. purpurascens*, *B. rubens*, *B. secalinus*, and *B. squarrosus* were the most favorable species. *Bromus brizaeformis*, *B. Gussonii*, and *B. velutinus* were apparently moderately susceptible. *Bromus carinatus*, *B. commutatus*, *B. interruptus*, and *B. racemosus* were apparently more or less resistant.

Negative results were obtained with *Bromus arduennensis*, *B. asper*, *B. breviaristatus*, *B. erectus*, *B. Griesoni*, *B. laxus*, *B. longiflorus*, *B. propendens*, *B. Pumpellianus*, *B. pungens*, *B. rigidus*, *B. segetum*, *B. sterilis*, *B. tectorum*, and *B. virens*.

Ward gives the results of the study of rust from several other species of Bromus which indicate the existence of other races.

He believed that the hosts of races could be changed through growing the rust on "bridging" species. His evidence, however, is not conclusive and may in part, at least, be explained by mixtures of races.

O. AECIA ON SPECIES OF PHACELIA

a. Results obtained from inoculations from telia on grasses to aecial hosts

Telia from Agropyron

1420. Collected on *Agropyron sp.*, June 14, 1920, at Atascadero, California, by E. Bethel. This was cultured on *Anchusa officinalis, Cerinthe minor, Cynoglossum officinale, Hydrophyllum virginianum, Phacelia californica, P. distans, P. tanacetifolia,* and *Phacelia sp.*, resulting in the development of pycnia on the last only.

11220. Collected on *Agropyron sp.*, June 6, 1920, at Mill Valley, California, by E. Bethel. This was sown on *Cynoglossum officinale, Hydrophyllum sp.*, and *Phacelia californica,* resulting in the development of pycnia on the last only.

13420. Collected on *Agropyron sp.*, Sept. 9, 1920, at Mill Valley, California, by E. Bethel. This was sown on *Cynoglossum officinale, Hydrophyllum virginianum, Lithospermum arvense, Myosotis alpestris, Onosmodium occidentale, Phacelia californica, P. distans,* and *P. tanacetifolia,* with production of pycnia and aecia on *P. californica* and pycnia on *P. distans.*

Telia from *Elymus condensatus*

30019. Overwintered telia collected on *Elymus condensatus,* March 23, 1920, at Monrovia, California, by E. Bethel. This was sown on *Anchusa officinalis, Hydrophyllum virginianum, Macrocalyx Nyctelea, Phacelia californica, P. distans,* and *P. tanacetifolia,* resulting in production of pycnia and aecia on *Phacelia distans* and pycnia on *P. tanacetifolia.*

30319. Overwintered telia collected on *Elymus condensatus,* March 20, 1920, at Pasadena, California, by E. Bethel. This was sown on *Anchusa officinalis, Cerinthe minor, Cynoglossum officinale, Hydrophyllum virginianum, Lithospermum arvense,*

Myosotis alpestris, Onosmodium occidentale, Phacelia californica, P. distans, and *P. tanacetifolia,* resulting in production of pycnia and aecia on *Phacelia distans* only.

b. Results obtained from inoculations from aecia on Phacelia to various species of grasses

Ph 5. Aecia on *Phacelia distans* collected Feb. 16, 1920, at Monrovia, California, by E. Bethel. Inoculations were made on *Agropyron caninum, A. Smithii, A. tenerum, Bromus altissimus, B. arvensis, B. brizaeformis, B. carinatus, B. ciliatus, B. commutatus, B. hordeaceus, B. inermis, B. japonicus, B. Kalmii, B. lanuginosus, B. latiglumis, B. madritensis, B. marginatus, B. mollis, B. orcuttianus, B. polyanthus, B. Porteri, B. pratensis, B. Pumpellianus, B. purgans, B. Richardsonii, B. rubens, B. secalinus, B. sitchensis, B. sterilis, B. tectorum, B. unioloides, B. villosus, B. vulgaris, Elymus canadensis, E. condensatus, E. virginicus, Hordeum Gussoneanum, H. jubatum,* and *H. murinum. Bromus brizaeformis, B. hordeaceus, B. lanuginosus, B. pratensis, B. secalinus, B. sterilis,* and *B. tectorum* were very susceptible. The others showed little or no infection.

Ph 13. From aecia on *Phacelia distans* produced from telia on *Elymus condensatus* (30319) from Pasadena, California. Inoculations were made on *Agropyron repens, A. Smithii, A. tenerum, Bromus arvensis, B. secalinus, B. inermis, B. macrostachys, B. mollis, B. Richardsonii, B. tectorum, Elymus arenarius, E. canadensis, E. condensatus, E. glaucus, E. virginicus, Hordeum jubatum, H. nodosum, H. pusillum, H. vulgare, Secale cereale,* and *Sitanion Hystrix.* Only *Elymus condensatus* proved to be susceptible.

From this evidence it is apparent that there are at least two races with aecia on Phacelia. These may be distinguished as follows:

48. **Puccinia rubigo-vera Phaceliae,** nov. sp. f.

Aecial hosts. — The culture was derived from aecia on *Phacelia distans* (Ph 5) from Monrovia, California.

Grass hosts. — *Bromus brizaeformis, B. hordeaceus, B. lanugi-*

nosus, B. pratensis, B. secalinus, B. sterilis, and *B. tectorum* are susceptible species.

Negative results or only a few, small uredinia occurred on *Agropyron caninum, A. Smithii, A. tenerum, Bromus altissimus, B. arvensis, B. carinatus, B. ciliatus, B. commutatus, B. inermis, B. japonicus, B. Kalmii, B. latiglumis, B. madritensis, B. marginatus, B. mollis, B. orcuttianus, B. polyanthus, B. Porteri, B. Pumpellianus, B. purgans, B. Richardsonii, B. rubens, B. sitchensis, B. unioloides, B. villosus, B. vulgaris, Elymus canadensis, E. condensatus, E. virginicus, Hordeum Gussoneanum, H. jubatum,* and *H. murinum.*

49. **Puccinia rubigo-vera** sp. f. **procera** (Dietel & Holw.), nov. comb.

Puccinia procera Dietel & Holw. Erythea, 1 : 249. 1893.

Aecial hosts. — Aecia of this race were produced on *Phacelia distans.* Pycnia occasionally were produced on *Phacelia tanacetifolia.*

Negative results were obtained with *Anchusa officinalis, Cerinthe minor, Cynoglossum officinale, Hydrophyllum virginianum, Lithospermum arvense, Macrocalyx Nyctelea, Myosotis alpestris, Onosmodium occidentale,* and *Phacelia californica.*

Grass hosts. — Only *Elymus condensatus* has been found to be susceptible.

Negative results were obtained with *Agropyron repens, A. Smithii, A. tenerum, Bromus arvensis, B. inermis, B. macrostachys, B. mollis, B. Richardsonii, B. secalinus, B. tectorum, Elymus arenarius, E. canadensis, E. glaucus, E. virginicus, Hordeum jubatum, H. nodosum, H. pusillum, H. vulgare, Secale cereale,* and *Sitanion Hystrix.*

This race has been collected only from California (30019, 30319, Ph 13). It has much larger urediniospores than the others in *Puccinia rubigo-vera* and perhaps should be retained as a species. On account of the evident relationship it is here included as a race.

P. AECIA ON SPECIES OF HYDROPHYLLUM

One collection of aecia (Hy 9), made by G. R. Hoerner on *Hydrophyllum sp.,* at Corvallis, Oregon, June 1, 1919, was sown

on a series of grasses, and the results indicate a distinct race. This race may be characterized as follows:

50. **Puccinia rubigo-vera Hydrophylli,** nov. sp. f.

Aecial hosts. — Only the host of the original collection, *Hydrophyllum sp.*, is so far known.

Grass hosts. — *Elymus glaucus* and *E. virginicus* were the most favorable species. *Hystrix Hystrix* was moderately susceptible. Negative results or only a few, small uredinia were obtained with *Agropyron caninum, A. desertorum, A. repens, A. Smithii, A. tenerum, Bromus ciliatus, B. Kalmii, B. secalinus, B. sterilis, B. villosus, Elymus canadensis, E. condensatus, E. robustus, Hordeum Gussoneanum, H. jubatum, H. murinum, H. nodosum, H. pusillum, H. vulgare, Sitanion Hystrix,* and *Triticum vulgare.*

Arthur (1916) found that aecia on *Hydrophyllum* (*capitatum*), sent by A. O. Garrett, from Salt Lake City, Utah, were connected with rust on *Agropyron tenerum. Elymus virginicus* was only slightly infected. Arthur considered this rust to be *Puccinia montanensis.* His identification was an error and was later corrected (Arthur, 1921) when he placed it in *Puccinia apocrypta* E. & T. This is apparently a race of *Puccinia rubigo-vera*, differing from *Hydrophylli* in the susceptibility of *Agropyron tenerum.*

Q. AECIA ON SPECIES OF IMPATIENS

a. Results obtained from inoculations from telia on grasses to aecial hosts

Telia on Agropyron

5518. Collected on *Agropyron sp.*, Aug. 23, 1918, at Freeville, New York, by H. S. Jackson. This was sown on *Anemone canadensis, Clematis virginiana, Impatiens biflora, Thalictrum aquilegifolium, T. dioicum, T. minus,* and *T. polygamum,* with production of pycnia and aecia on *Impatiens biflora* only.

18019. Collected on *Agropyron tenerum,* Aug. 8, 1919, at Dauphin, Manitoba, by W. P. Fraser. This was sown on *Impatiens biflora,* with production of pycnia and aecia.

21319. Telia produced in the greenhouse, Sept. 30, 1919, on

Agropyron tenerum from rust received from W. P. Fraser from Dauphin, Manitoba, on *Hordeum jubatum* (Ho 24).

Telia on Elymus

5718. Collected on *Elymus sp.*, Aug. 23, 1918, at Coyglen, New York, by H. S. Jackson. This was sown on *Anemone canadensis*, *A. cylindrica*, *Clematis orientalis*, *C. virginiana*, *Impatiens biflora*, and *Thalictrum dioicum*, with production of pycnia and aecia on *Impatiens biflora* only.

13719. Collected on *Elymus sp.*, Aug. 5, 1919, at Jackson, Tennessee, by C. A. Ludwig. This was sown on *Impatiens biflora*, producing pycnia and aecia.

16419. Collected on *Elymus virginicus*, Aug. 25, 1919, at New Haven, Indiana, by L. S. Cheney. This was sown on *Clematis virginiana*, *Impatiens biflora*, and *Thalictrum dioicum*, with production of pycnia and aecia on *Clematis virginiana* and *Impatiens biflora*. The telia of two races were mixed in this collection.

19419. Collected on *Elymus virginicus*, Sept. 17, 1919, at Salem, Indiana, by L. S. Cheney. This was sown on *Impatiens biflora*, with production of pycnia and aecia.

20819. Telia developed in the greenhouse, Sept. 24, 1919, on *Elymus virginicus*, by a culture produced from uredinia collected on *E. virginicus* at Jackson, Tennessee (El 33). These were sown on *Impatiens biflora*, with production of pycnia and aecia.

21219. Telia developed in the greenhouse, Sept. 30, 1919, on *Elymus canadensis*, by a culture produced from uredinia collected on *Hordeum jubatum* (Ho 24) at Dauphin, Manitoba. These were sown on *Impatiens biflora*, with production of pycnia and aecia.

21619. Telia developed in the greenhouse, Sept. 30, 1919, on *Elymus canadensis*, by a culture produced from uredinia (El 34) collected on *E. canadensis* at Jackson, Tennessee. These were sown on *Impatiens biflora*, with production of pycnia and aecia.

22619. Telia developed in the greenhouse, Oct. 17, 1919, on *Hordeum jubatum*, by a culture produced from uredinia (Ho 24) collected on *Hordeum jubatum* at Dauphin, Manitoba. These

were sown on *Impatiens biflora*, with production of pycnia and aecia.

24019. Collected on *Elymus virginicus*, Sept. 23, 1919, at Ann Arbor, Michigan, by the writer. This was sown on *Impatiens biflora*, with production of pycnia and aecia.

24119. Collected on *Elymus canadensis*, Sept. 23, 1919, at Ann Arbor, Michigan, by the writer. This was sown on *Impatiens biflora*, with production of pycnia and aecia.

Telia on *Hystrix Hystrix*

23619. Collected on *Hystrix Hystrix*, Oct. 21, 1919, at Ann Arbor, Michigan, by the writer. This was sown on *Impatiens biflora*, with production of pycnia and aecia.

b. Results obtained by inoculating species of grasses with races connected with aecia on Impatiens

The following collections were used with the results given in Table XVII:

El 33. Uredinia collected on *Elymus virginicus*, June 3, 1919, at Jackson, Tennessee, by C. A. Ludwig. The telia produced on *Elymus virginicus* by this culture were sown on *Impatiens biflora*, producing aecia (see 20819).

El 34. Uredinia collected on *Elymus canadensis*, Aug. 5, 1919, at Jackson, Tennessee, by C. A. Ludwig. The telia produced on *Elymus canadensis* by this culture were sown on *Impatiens biflora*, producing aecia (see 21619).

Ho 24. Uredinia collected on *Hordeum jubatum*, Aug. 8, 1919, at Dauphin, Manitoba, by W. P. Fraser. The telia produced on both *Agropyron tenerum* (21319) and *Elymus canadensis* (21219) were sown on *Impatiens biflora*, producing aecia.

I 1. Aecia collected on *Impatiens sp.*, June 11, 1919, at Lafayette, Indiana, by F. B. Fuller.

I 3. Aecia collected on *Impatiens sp.*, June 23, 1919, at Lafayette, Indiana, by F. B. Fuller.

I 5. Aecia produced on *Impatiens biflora* in greenhouse at Lafayette, Indiana, from telia collected on *Elymus virginicus* (16419) at New Haven, Indiana.

I 6. Aecia produced on *Impatiens biflora* in greenhouse at Lafayette, Indiana, from telia on *Elymus canadensis* (21619) from culture El 34.

I 8. Aecia produced on *Impatiens biflora* in greenhouse at Lafayette, Indiana, from telia on *Hordeum jubatum* (22619) from culture Ho 24.

I 9. Aecia produced on *Impatiens biflora* in greenhouse at Lafayette, Indiana, from telia on *Agropyron tenerum* (21319) from culture Ho 24.

I 12. Aecia produced on *Impatiens biflora* in greenhouse at Lafayette, Indiana, from telia (13719) collected on *Elymus sp.* at Jackson, Tennessee.

I 13. Aecia produced on *Impatiens biflora* in greenhouse at Lafayette, Indiana, from telia (24019) obtained on *Elymus virginicus* collected at Ann Arbor, Michigan.

I 14. Aecia produced on *Impatiens biflora* in greenhouse at Lafayette, Indiana, from telia (24119) on *Elymus canadensis* collected at Ann Arbor, Michigan.

c. Summary of races of Puccinia rubigo-vera with aecia on Impatiens

As is shown in Table XVII, four races have been distinguished by having aecia on Impatiens. These may be designated as follows:

51. **Puccinia rubigo-vera** sp. f. **Impatientis** (Arth.), nov. comb.
Puccinia Impatientis Arth. Bot. Gaz., 35 : 19. 1903.

Arthur (1903, 1904, 1905, 1910) connected rust on *Elymus canadensis, E. striatus,* and *E. virginicus* with aecia on *Impatiens pallida* (*I. aurea*). *Actaea alba, Boehmeria cylindrica* (L.) Sw., *Callirrhoe involucrata, Caulophyllum thalictroides* (L.) Michx., *Dirca palustris* L., *Hydrophyllum virginicum, Ipomoea pandurata* (L.) G. F. W. Mey., *Mimulus ringens* L., *Myosotis palustris, Napaea dioica* L., *Polemonium reptans, Polygala Senega* L., *Psoralea Onobrychis* Nutt., and *Thalictrum dioicum* gave negative results.

TABLE XVII

REACTION OF SPECIES OF GRASSES TO RACES OF *PUCCINIA RUBIGO-VERA* WITH AECIA ON IMPATIENS

Species inoculated	Race Impatientis					Race similis				Race graminicola		Race singularis
	El 33*	El 34	I 5	I 6	I 13	Ho 24	I 3	I 8	I 9	I 1	I 12	I 14
Agropyron caninum	t	t	+	..	+	+	−	+	+	+++	+++	+
pseudorepens	−	t	..	..	..	..	..	..	..	..	..	..
repens	−	..	..	..	−	−	−	−	−	−	..	−
Smithii	..	..	..	..	..	−	..	..	..	−	..	..
tenerum	t	t	+	++	+	..	+	++	++	t	t	++ +
Bromus carinatus	..	..	..	..	..	−	−	..	..	..	..	..
ciliatus	−	..	..	..	..	−	−	..	..	−	..	..
Kalmii	..	..	..	..	..	..	−	..	..	−	..	..
polyanthus	..	..	..	..	..	−	−	..	..	..	..	..
Elymus australis	+	+	+	+	+	−	t	t	..	t	+	+
canadensis	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++
condensatus	..	..	..	..	..	..	t	..	..	t	..	..
glaucus	+	−	−	+	+	−	t	+	..	+	+	+
robustus	t	..	..	..	..	+	+	..	..	t	..	..
striatus	..	..	..	+++	++	..	..	++	+	..	..	−
virginicus	+++	+++†	+++	+++	+++	+++	+++	++	..	++	++	+
Hordeum Gussoneanum	..	..	..	..	..	+	..	..	..	−	..	..
jubatum	+	t	+	−	+	+++	+++	+++	+++	+++	+++	−
murinum	−	..	..	−	..	−	−	..	..	−	..	..
nodosum	+	..	+	+	+	+	..	++	..	++	+	t
pusillum	+	t	−	+	+	++	++	++	..	++	+	t
vulgare	t	..	..	−	..	−	−	..	..	−	−	−
Hystrix Hystrix	−	..	−	t	−	t	−	−	−	−	−	−
Secale cereale	−	−	..	−	..	−	−	−	..	+	..	−
Sitanion Hystrix	+	..	+	+	+	t	t	..	..	++	..	t
Trisetum spicatum	..	..	..	..	..	..	−	..	..	−	..	..
Triticum vulgare	−	−	−	−	..	−	−	−	−	+	−	−

* Accession number of collection. For data see text.

† One collection of *Elymus virginicus* was resistant. It was, however, susceptible to other cultures of the race.

Fraser (1920), using aecia from *Impatiens biflora* collected at Hudson, Province of Quebec, obtained abundant infection on *Elymus canadensis* and *E. virginicus*, slight infection of *Hordeum jubatum*, and negative results with *Hystrix Hystrix*. These probably belong with cultures El 33–20819, El 34–21619–I 6, 16419–I 5, and 24019–I 13, in the race here designated as *Impatientis*. The species infected are as follows:

Aecial hosts. — *Impatiens biflora* and *I. pallida* are the only species which have been shown by cultures to be aecial hosts.

Grass hosts. — *Elymus canadensis*, *E. virginicus*, and possibly *E. striatus* are the most favorable grass hosts.

Negative results or only a few, small uredinia were obtained with *Agropyron caninum*, *A. pseudorepens*, *A. repens*, *A. Smithii*, *A. tenerum*, *Bromus ciliatus*, *Elymus australis*, *E. glaucus*, *E. robustus*, *Hordeum jubatum*, *H. murinum*, *H. nodosum*, *H. pusillum*, *H. vulgare*, *Hystrix Hystrix*, *Secale cereale*, *Sitanion Hystrix*, and *Triticum vulgare*.

This race has been obtained from Tennessee, Indiana, Missouri, Michigan, and Province of Quebec.

52. Puccinia rubigo-vera similis, nov. sp. f.

From aecia on *Impatiens biflora* collected at Dauphin, Manitoba, Fraser obtained abundant infection on *Hordeum jubatum* and somewhat less infection on *Elymus canadensis* and *E. virginicus*. A slight infection was obtained on *Agropyron tenerum*, *A. Richardsonii*, and *Hystrix Hystrix* (*H. patula*).

Negative results were obtained with *Triticum vulgare*. The results obtained with material supplied by Fraser (Ho 24–21319–22219–I 8–I 9) agree very well with his results. Only one other collection of this race (I 3 from Lafayette, Indiana) has been studied.

Aecial host. — *Impatiens biflora.*

Grass hosts. — *Elymus canadensis*, *E. virginicus*, and *Hordeum jubatum* are the most favorable species. *Hordeum pusillum* and possibly *H. nodosum* and *Elymus striatus* were moderately infected.

Negative results or only a few, small uredinia were obtained

with *Agropyron caninum, A. repens, A. Richardsonii, A. Smithii, A. tenerum, Bromus carinatus, B. ciliatus, B. Kalmii, B. polyanthus, Elymus australis, E. condensatus, E. glaucus, E. robustus, Hordeum Gussoneanum, H. murinum, H. vulgare, Hystrix Hystrix, Secale cereale, Sitanion Hystrix, Trisetum spicatum,* and *Triticum vulgare.*

53. **Puccinia rubigo-vera graminicola,** nov. sp. f.

Aecial host. — Impatiens biflora.

Grass hosts. — Agropyron caninum, Elymus canadensis, and *Hordeum jubatum* were the most favorable species. *Elymus virginicus* and possibly *Hordeum nodosum, H. pusillum,* and *Sitanion Hystrix* were moderately susceptible.

Negative results or only a few, small uredinia were obtained with *Agropyron repens, A. Smithii, A. tenerum, Bromus ciliatus, B. Kalmii, Elymus australis, E. condensatus, E. glaucus, E. robustus, Hordeum Gussoneanum, H. murinum, H. vulgare, Hystrix Hystrix, Secale cereale, Trisetum spicatum,* and *Triticum vulgare.*

This race was obtained from Indiana (I 1) and Tennessee (13719–I 12).

54. **Puccinia rubigo-vera singularis,** nov. sp. f.

Aecial host. — Impatiens biflora.

Grass hosts. — Agropyron tenerum and *Elymus canadensis* were the most favorable species.

Negative results or only a few, small uredinia were obtained with *Agropyron caninum, A. repens, Elymus australis, E. glaucus, E. striatus, E. virginicus, Hordeum jubatum, H. nodosum, H. pusillum, H. vulgare, Hystrix Hystrix, Secale cereale, Sitanion Hystrix,* and *Triticum vulgare.*

One collection (24119–I 14) of this race has been studied from Michigan.

d. Other races with aecia on Impatiens

Impatiens biflora — Hystrix Hystrix.

Since the races described above did not infect *Hystrix Hystrix,* the results obtained with collection 23619 (section Q *a*) indicate

that there is a race for which *Hystrix Hystrix* is a susceptible host.

R. RACES WITH AECIA UNKNOWN

The results of Eriksson's studies show that there are two other races which may be designated as follows:

55. **Puccinia rubigo-vera** sp. f. **holcina** (Erikss.), nov. comb. *Puccinia holcina* Erikss. Ann. Sci. Nat., Eighth Ser., 9 : 274. 1899.

Aecial hosts. — Unknown.

Grass hosts. — Eriksson (1899) inoculated *Agrostis stolonifera, Alopecurus pratensis, Avena sativa, Festuca elatior, Holcus lanatus, Lolium perenne, Secale cereale,* and *Triticum vulgare.* Infection was obtained on *Holcus lanatus* only. Eriksson considered this a distinct species and named it *Puccinia holcina.*

56. **Puccinia rubigo-vera** sp. f. **Triseti** (Erikss.), nov. comb. *Puccinia Triseti* Erikss. Ann. Sci. Nat., Eighth Ser., 9 : 277. 1899.

Aecial hosts. — Unknown.

Grass hosts. — Eriksson (1899) sowed urediniospores from *Trisetum flavescens* on *Agropyron* (*Triticum*) *repens, Bromus brizaeformis, Holcus lanatus, Secale cereale,* and *Triticum vulgare* with negative results. He considered this a distinct species and named it *Puccinia Triseti.* The results of Fischer and Mayor (1924), who connected a rust on *Trisetum distichophyllum* with aecia on *Thalictrum foetidum,* suggest species of Thalictrum as aecial hosts for this race.

IV. Discussion

It is evident that *Puccinia rubigo-vera,* as here conceived, is divided into a number of races on the basis of host specialization. In this paper fifty-six such races have been recognized. In addition there is evidence indicating the existence of twenty-one other races. For the most part these races are sharply limited in their specialization to aecial hosts, usually being restricted to only a few species of a genus. Thus race *Puccinelliae* is ap-

parently restricted to *Ranunculus Cymbalaria;* race *Secalis,* to a few species of Anchusa; race *orientalis,* to one or at the most a few species of Clematis, etc. In the race *Aquilegiae* several species of Aquilegia were found to be favorable hosts of the aecial stage, and it is probable that this race has a wide range within the genus Aquilegia.

Only a few of the races produce aecia on species of more than one genus. Müller showed that the race *Symphyti-Bromorum* produced aecia on *Symphytum officinalis* and *Pulmonaria montana.* The race with the most aecial hosts is *Actaeae-Elymi,* which, as Mayor has shown, produces aecia on twenty-nine species of the genera Aconitum, Actaea, Adonis, Aquilegia, Delphinium, Eranthis, Helleborus, and Nigella. The race *Onosmodii* is of special interest in this connection since it produces aecia on *Macrocalyx Nyctelea* in the Hydrophyllaceae and *Onosmodium occidentale* in the Boraginaceae.

The specialization of races to grass hosts exhibits similar differences. The race *persistens* is apparently restricted to *Agropyron repens;* the races *circumscripta* and *alpina* to *Hordeum jubatum;* the race *virginica* to *Elymus virginicus;* the races *californica* and *procera* to *Elymus condensatus,* etc. The race *Tritici* develops on only a few species of *Triticum;* the race *Secalis,* on two species of *Secale.* A number of the races, however, have favorable hosts in several genera of the grasses. Thus the race *elymicola* infects seven species of the genera Elymus, Hordeum, and Hystrix; the race *canadensis* six species of Agropyron, Elymus, and Hystrix.

In no case, however, has the range of grass hosts included species in more than one tribe of the Poaceae. It is noticeable that most of the races are found on genera of the Hordeae.

It is interesting to note that a race narrowly specialized to a few species for its aecial hosts may have a much wider range for hosts of its uredinial stage. Thus the race *elymicola* is probably restricted to a few species of Thalictrum for its aecial hosts and infects seven species of Elymus, Hordeum, and Hystrix in its uredinial stage. The race *graminicola* produces aecia on *Impatiens biflora* and uredinia on species of Agropyron, Elymus, and Hordeum.

The reverse also occurs. Thus the race *Actaeae-Elymi*, as already stated, produces aecia on twenty-nine species of nine genera. It is apparently restricted, however, to *Elymus europaeus* for its uredinial stage.

Several of the races are rather narrowly restricted to a few species in both stages. Thus the race *Puccinelliae* is restricted to *Ranunculus Cymbalaria* for its aecial stage and to *Puccinellia airoides* for its uredinial stage. None of the races have so far been shown to have a wide host range for both stages.

A number of interesting parallelisms exist in this group of races. Thus the race *Actaeae-Agropyri* has been shown by Mayor to have a very similar wide range of aecial hosts to *Actaeae-Elymi;* the former, however, is closely restricted to *Agropyron caninum* for its grass host and the latter is closely restricted to *Elymus europaeus.*

Also the groups with aecia on Thalictrum, Clematis, and Impatiens, which have received the most study, show a very similar series of grass hosts, mostly species of Agropyron, Elymus, Hordeum, Hystrix, and, except for Impatiens, Bromus. The corresponding races of each of these aecial groups show certain similarities, although only a few are exactly alike in grass host specialization. This may indicate that as the races of *Puccinia rubigo-vera* developed through specialization to Clematis, Thalictrum, Impatiens, etc., differentiation by specialization to species of grasses was also taking place in each of these lines of development.

This parallelism extends to those closely related species or possibly extreme forms of *Puccinia rubigo-vera*, *Puccinia Elymi*, and *P. tomipara* which have multicellular teliospores. *Puccinia Elymi* apparently has aecia on species of Thalictrum and evidently contains one race on *Elymus arenarius* and another on *Agropyron cristatum*. *Puccinia tomipara*, with aecia on *Thalictrum dasycarpum*, is restricted to *Bromus ciliatus* and *Bromus latiglumis.*

The closely related species *Puccinia Eatoniae* Arth., which differs mostly from *Puccinia rubigo-vera* in that its aecia arise from a systemic mycelium, also shows a marked parallelism in its host specialization in that its two varieties are distinguished

(Mains, 1932) by the production of aecia on a ranunculaceous species (*Ranunculus abortivus*) in one case and on a boraginaceous species (*Myosotis virginica*) in the other.

It has been shown that the race *Tritici* can be still further divided into smaller units by means of differences in host specialization. By the use of a selected set of wheat varieties fifty-three physiologic forms of this race have been distinguished by the reactions of the varieties when inoculated with these forms. So far in this study only slight evidence has been obtained of similar separations within the other races. Thus one collection of *Hordeum jubatum* apparently was resistant to culture Th 15 of the race *vulgaris* (Table II) and to race *occidentalis* (Table III) and susceptible to other cultures of these races. Likewise, one collection of *Elymus virginicus* was apparently resistant to one culture of race *anomala* (Table II) and to one of race *Impatientis* (Table XIII), though susceptible to the other cultures of these races. Though these instances are hardly sufficient to justify conclusions, they suggest that some at least of the wild grass races may be subdivided through differences in reaction of selections or strains of the various species of grasses. There is no reason to assume that the races with wild grass hosts differ in this respect from the race *Tritici* on wheat. The last has received extensive study in this regard, but too few collections of both the wild grass races and their hosts have been studied to justify a comparison.

Although the races of *Puccinia rubigo-vera* show no marked morphological differences, yet there is a certain amount of variation, mostly in spore size. Arthur and Fromme (1920) have attempted to distinguish the races with aecia on *Impatiens* (*Dicaeoma Impatientis*) from those with aecia on the Ranunculaceae (*Dicaeoma Clematidis*) by the smaller size of uredinio-spores. In this regard the former do not differ from many races with aecia on Ranunculaceae, specially those having aecia on Thalictrum. They, however, are somewhat outstanding as a group for small size of teliospores, 10–19 × 29–45 μ. However, the races *anomala* and *persistens* with aecia on Thalictrum, *indianensis* with aecia on Clematis, *dakotensis* with aecia on Anemone,

obliterata with aecia on Aquilegia, *Actaeae-Elymi* and *septentrionalis* with aecia on Actaea, *Onosmodii* with aecia on Onosmodium and Macrocalyx, and *Hydrophylli* with aecia on Hydrophyllum do not differ to any appreciable extent in this regard (width 13–18 μ). The other races show diverse variations in size of the teliospores. Thus races *elymicola* (10–16 × 32–50 μ), *virginica* (14–17 × 32–48 μ), *circumscripta* (10–19 × 34–55 μ), *Betheli* (13–16 × 45–64 μ), and *Delphinii* (13–21 × 45–64 μ) are examples of the races with teliospores of moderate size. The maximum is apparently reached in such races as *coloradensis* (14–19 × 55–83 μ), *californica* (16–23 × 51–71 μ), and *procera* (15–21 × 45–79 μ).

Somewhat similar differences exist in regard to the urediniospores, although there is not quite so much variation. Races *indianensis* (16–17 × 17–21 μ), *dakotensis* (16–18 × 19–22 μ), *Hydrophylli* (13–17 × 19–23 μ), and *elymicola* (16–18 × 19–23 μ) are examples of those with smaller urediniospores. Races *graminicola* (18–22 × 23–32 μ), *californica* (23–26 × 23–32 μ), and *Delphinii* (19–23 × 23–34 μ) illustrate those with moderate-sized urediniospores. The race *procera* (25–32 × 34–40 μ) is outstanding for its large urediniospores.

There is also some variation in the size of the aeciospores and in the size, shape, and wall thickness of the peridial cells, but there seems to be no consistent correlation with host genera.

It would seem, therefore, that the races of this species intergrade to such an extent that most of them cannot be distinguished morphologically with any degree of certainty. Most of them can be distinguished with much greater accuracy by their host specialization. Many are sharply differentiated in this way. It seems best, therefore, to consider these as included in one species and to recognize as races the groups separated largely by host specialization. It is obvious that, if the latter are considered species, there will be a multiplication of species to a point where such a classification would lose its value.

V. Summary

In this study it has been shown that aecia on species of Thalictrum are connected with rust on species of Agropyron, Bromus,

Elymus, Hordeum, Hystrix, and Triticum; on Clematis, with rust on species of Agropyron, Elymus, Bromus, Hordeum, and Hystrix; on Anemone, with rust on species of Agropyron, Elymus, and Hordeum; on Aquilegia, with rust on species of Elymus; on Delphinium, with rust on *Agropyron tenerum;* on Ranunculus, with rust on species of Hordeum, Poa, and Puccinellia; on Anchusa, with rust on species of Secale; on Onosmodium and Macrocalyx, with rust on species of Agropyron and Elymus; on Phacelia, with rust on species of Bromus and Elymus; on Hydrophyllum, with rust on species of Elymus and Hystrix; on Impatiens, with rust on species of Agropyron, Elymus, Hordeum, and Hystrix.

Fifty-six races are recognized in *Puccinia rubigo-vera*, distinguished by differences in their host specialization. *Puccinia alternans, P. persistens, P. triticina, P. Agrostidis, P. obliterata, P. perplexans, P. Actaeae-Agropyri, P. Actaeae-Elymi, P. Aconiti-rubrae, P. Dietrichiana, P. dispersa* (*P. secalina*), *P. Symphyti-Bromorum, P. bromina, P. procera,* and *P. Impatientis* are considered to be races of *Puccinia rubigo-vera.*

The following indexes will serve to locate the summary of results for the various races treated in these studies:

A. AECIAL HOSTS OF RACES OF *PUCCINIA RUBIGO-VERA*

The numbers refer to the races so designated under Section III. A number in parenthesis indicates a doubtful host for that race, usually being only moderately susceptible. In some cases in which races are uncertain, reference is given by subsection, such as Ae, or to comment under a race by "see under."

Aconitum Anthora 35
Lycoctonum 34 35
Napellus 35 37
paniculatum 34 35 37
pyrenaicum 35
Stoerkianum 35 37
variegatum 35 37
Actaea alba 36
cimicifuga 35
rubra 36
spicata 24 34 35
Adonis aestivalis 35
annua 35
Anchusa arvensis 39
capensis 39
officinalis 39
Anemone cylindrica 22
globosa 22 23
Hepatica 24 25
sp. 26

Anemonella thalictroides (10)
Aquilegia alpina 28
californica Dc
canadensis 27 29 Dc
chrysantha Dc
coerulea 27 Dc
glandulosa 35
Skinneri Dc
vulgaris 27 28 Dc

Clematis Douglasii Bd
Drummondii Bd
lanuginosa 15
ligusticifolia 15 16 17 Bd
pseudoflammula Bd
virginiana 11 12 13 14 20 Bd
vitalba Bd
sp. 18 19 21

Delphinium Ajacis 35
cashmirianum 35
Consolida 34 35
dictyocarpum 35
elatum 35
exaltatum 35
Geyeri 30
Nelsoni 30
nudicaule 35
Staphysagria 35
sp. 30

Eranthis hiemalis 35

Helleborus caucasicus 35
foetidus 25 34 35
niger 35
viridis 35
Hepatica triloba 24 25
Hydrophyllum sp. 50

Impatiens biflora 51 52 53 54 Qd
pallida 51

Leptopyrum fumarioides 35
Lithospermum arvense 42

Macrocalyx Nyctelea 40
Myosotis sylvatica 42

Nigella arvensis 35
damascena 25 34 35
gallica 35

Onosmodium occidentale 40

Phacelia californica Oa
distans 48 49 Oa
Pulmonaria montana 41

Ranunculus acris 33
californicus See under 31
Cymbalaria 31 32

Symphytum officinale 41

Thalictrum alpinum Ae
aquilegifolium 1 4 Ae
dasycarpum 1 2 3 4 6 Af
Delavayi 9 10
dioicum 1 4 8 Ae
elatum 10
exaltatum 10
Fendleri 5 Ae
flavum 9 10
foetidum Ae
glaucum 10
lucidum 10
majus Ae
minus 9 (10) Ae Af
nutans 10
paniculatum 1 4
polygamum 1
ruthenicum 10
sparsiflorum 8
tuberosum 10
sp. 7 8
Trollius europaeus 38

B. UREDINIAL AND TELIAL HOSTS OF RACES OF *PUCCINIA RUBIGO-VERA*

Aegilops crassa 10
Agropyron caninum (23) 24 34 38 53 Ae
cristatum Ae Af Bd
dasystachum 22
glaucum Bd
prostratum Bd
pseudorepens (9) Bd
repens 9 Bd
Richardsonii 22
Smithii 40 Bd
spicatum 22
tenerum 19 22 23 30 54 See also 50
violaceum 29 Ae
sp. Oa
Agrostis alba 28
borealis Ae
vulgaris 28
Alopecurus pratensis 33
brachystachys 33
Avena elatior 33

Bromus adoensis 47
arduennensis 43 46
arduennensis var. villosus (44) 46
arvensis 39 41 43 45 47
asper 43
brachystachys 41 45 46 47
brizaeformis 43 (45) (46) (47) 48
carinatus 8 21
ciliatus 20 Af
erectus 41
grossus (46)
Gussonii (44) (47)
hordeaceus 46 47 48
inermis 41 42
interruptus (46)
Kalmii Bd
Krausii 46
lanuginosus 48
latiglumis Af
macrostachys 41 43 45 47
madritensis (44) 47
mollis 41 43 (45) 46 47
multiflorus (46)
patulus 43 45 47
pendulinus (44) 45 (46) 47
polyanthus 21
Porteri 8 Bd
pratensis 48
Pumpellianus (8)
purgans 20
purpurascens 44 45 47
racemosus 43
Richardsonii 8
rubens 44 45 47
secalinus 41 43 45 (46) 47 48
sitchensis 8 21
squarrosus 42 43 45 46 47
squarrosus var. villosus 46
sterilis 43 44 48
tectorum 42 43 48
velutinus (45) (46) (47)
vestitus 46

Elymus arenarius Af
canadensis 1 3 6 7 13 14 15 22 26 27 36 51 52 53 54
condensatus 7 16 (40) 49
diversiglumis (22)
europaeus 25 35
glaucus 6 7 17 18 (23) 50
glaucus Jepsoni Dc
robustus (1) 6 7 27
striatus 6 (51) (52)
triticoides Bd
virginicus 2 3 6 11 12 13 15 (22) 36 50 51 52 (53) Bd

Festuca rubra commutata 37
rubra violacea 37
Thurberi Ae

Holcus lanatus 55
Hordeum Gussoneanum 6 (11) (14) 17 (19)
jubatum 1 2 3 4 5 7 11 13 18 26 32 52 53 Bd
nodosum (2) 5 26 (52)
pusillum (7) (52)
Hystrix Hystrix 6 11 (13) (22) 36 (50) Qd

Poa nemoralis firmula Ae
sp. See under 31
Puccinellia airoides 31

Secale cereale 39
montanum 39

Trisetum distichophyllum Ae
flavescens 56
Triticum compactum 10
spelta 10
vulgare 10

C. RACES OF *PUCCINIA RUBIGO-VERA*, THEIR SYNONYMS AND RELATED SPECIES

Puccinia Aconiti-rubrae 37
Actaeae-Agropyri 34
Actaeae-Agropyri sp. f. Actaeae-Elymi 35
Hepaticae-Agropyri 24
Hepaticae-Elymi 25
typica 34
Actaeae-Elymi 35
Agropyri Bd
agropyrina 9
Agrostidis 28
alternans 8
apocrypta See under 50
borealis Ae
bromina 43
cinera See under 31
Cockerelliana Ae
Dietrichiana 38
dispersa 39
dispersa sp. f. Agropyri 9
Bromi 43
Secalis 39
Tritici 10
Elymi Ae Af
holcina 55
Impatientis 51
obliterata 29 Ae
perplexans 33
persistens 9 Ae
procera 49
Puccinia rubigo-vera sp. f. Aconiti-rubrae 37
Actaeae-Agropyri 34
Actaeae-Elymi 35
Agrostidis 28
alpina 32
alternans 8
anemonicola 26
anomala 2
Aquilegiae 27
Arthuri 20
arvensis 45
Betheli 14
Bromi 43
bromicola 21
californica 16
canadensis 22
circumscripta 4
clematidicola 17
coloradensis 15
dakotensis 23
Delphinii 30
Dietrichiana 38
elymicola 6

Puccinia rubigo-vera sp. f. Fraseri 3
graminicola 53
Hepaticae-Agropyri 24
Hepaticae-Elymi 25
holcina 55
hordeicola 5
Hydrophylli 50
Impatientis 51
indianensis 13
Lithospermi 42
montanensis 19
obliterata 29
occidentalis 7
Onosmodii 40
oregonensis 18
orientalis 11
perplexans 33
persistens 9
Phaceliae 48
procera 49
Puccinelliae 31
Secalis 39
septentrionalis 36
singularis 54
similis 52
Stenobromi 44
Symphyti-Bromorum 41
Triseti 56
Tritici 10
virginica 12
vulgaris 1
Wardii 47
Zeobromi 46
Puccinia secalina 39
Symphyti-Bromorum 41
Thalictri-distichophylli Ac
tomipara Af
Triseti 56
triticina 10

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NOTES ON ALGAE FROM THE TROPICAL ATLANTIC OCEAN. II

WM. RANDOLPH TAYLOR*

UNDER a similar title the writer published in 1929 (4) a group of annotated lists of marine algae from Jamaica, Tobago, Trinidad, Venezuela, and Panama. Except in some form such as the present it is difficult to assemble the slowly accumulating records of algal distribution in the American tropics, based as some are on small and old collections with a minimum of data. Since our knowledge of the algae of this region is really quite fragmentary, it is of importance that new and isolated stations for even the commonplace algae be put on record, so that the gaps in our accounts of distribution may gradually be closed. Until well-trained phycologists are able to get into the territory to collect carefully and widely, our information must come from collections made by botanists primarily otherwise concerned, but able to bring back a few score specimens as an incidental activity. Although the condition in which some of these reach the investigator induces more despair than pleasure, and although much is indeterminable, others — as in part of the material in the present report — are so well selected and dried that the study of them is thoroughly satisfying.

The present lists involve material from Jamaica, Haiti, and Costa Rica, for access to which the writer is indebted to the collectors and to others through whose hands it has reached him. Dr. M. A. Howe has kindly ventured a helpful opinion on some troublesome specimens. For Jamaica the list adds a few species to the known flora. Haitian records of species are increased more than 50 per cent, with many new stations, for the marine flora of

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this republic is as yet little studied. The records for Costa Rica are probably all new and represent an important accession to our rudimentary knowledge of the algae of the Central American mainland coast.

Marine Algae from Costa Rica

The writer acknowledges indebtedness to Dr. Carroll W. Dodge for the opportunity to inspect and determine a small and very interesting assortment of algae, collected for the most part from a coral reef off Piuta Point, two kilometers northwest of Puerto Limon, on the Atlantic coast of Costa Rica. These specimens were prepared by C. W. and B. W. Dodge and W. S. Thomas on March 20, 1930. The items are characteristic of the habitat and of the western tropical Atlantic; so far as the writer is aware, no other considerable collection has been reported upon from Costa Rica; the nearest collections in point of origin probably are those made by Dr. Dodge from the Panamanian coast and reported by the writer (4). With the exception of a small Caulerpa, nothing is particularly worthy of descriptive note, and the chief value of the collection is its contribution to our records of mainland distribution.

myxophyceae

Phormidium persicinum (Rke.) Gom.

Mastigocoleus testarum Lagerh.

chlorophyceae

Ulva fasciata Delile.

Chaetomorpha media (C. Ag.) Kg.

Halimeda Opuntia (L.) Lamx.

Caulerpa racemosa var. clavifera (Turn.) W.–v. B.

Caulerpa racemosa var. uvifera (Turn.) W.–v. B.

Caulerpa sertularioides (Gmel.) Howe.

Caulerpa Vickersiae Børg. var. **furcifolia** nov. var. (Pl. XXXVI) — Plant small, tufted to spreading, the branching rhizome not markedly differentiated from the other axes, repent or ascending, for the most part green, 125–215 μ in diameter, occasionally

bearing a few ramuli and frequently bearing descending rhizoidal branches; erect branches from the rhizome 60–85 μ in diameter, 4–7 (perhaps to 10) millimeters high, simple or generally 1–4 times subdichotomously divided, naked below or with a few, generally pinnate, simple thick-walled ramuli 65–95 μ in diameter, 250–350 μ long; ramuli mostly on the upper branches, or generally disposed except near their bases, walls thin, very slightly contracted toward the ramular bases, rarely simple and fairly evenly placed in simple pinnate arrangement, 65–85 μ in diameter, 300–390 μ long, or generally and characteristically irregularly and radially disposed, not pinnate, often clustered and occasionally subverticillate, 1–2 (occasionally 3) times subdichotomously forked, 50–85 μ in diameter, 170–300 μ long.

The plant grew in seeming abundance, among and overshadowed by *Wrangelia Argus* on a coral reef, Piuta Point, 2 kilometers northwest of Puerto Limon, Costa Rica, and was collected on March 20, 1930.

Caulerpa Vickersiae Børg. var. **furcifolia** nov. var. (Pl. XXXVI). — Planta parva penicillatim vel patenter fruticulosa; rhizomis 125–215 μ crassis, axibus aliis valde similibus, repentibus vel ascendentibus saepissime viridibus, interdum ramulos paucos ferentibus et saepe ramis retrorsis rhizoideis praeditis. Rami erecti e rhizoma nati 60–85 μ crassi, 4–7 (raro 10) mm. alti vel simplices vel semel ad quater subdichotome furcati, deorsum nudi vel paucos ramulos pinnatim ordinatos simplices, parietibus crassis, 65–95 μ crassos 250–350 μ longos ferentibus, sursum ramosi. Ramuli superiores parietibus tenuibus praediti plerumque ex parte ramorum erectorum superiore nati vel subaequiformiter dispositi et solum deorsum deficientes, paulum ad basin versus contracti, raro simplices et regulariter pinnati, 65–85 μ crassi, 300–390 μ longi, vel plerumque irregulariter et radiatim dispositi, nec pinnati, saepe fastigiati, raro subverticillati, semel, bis, vel rarius ter bifurcati, 50–85 μ crassi, 170–300 μ longi.

Abunde crescit inter plantas altiores Wrangeliae Argi in rupibus submarinis corallinis loco dicto Piuta Point, prope Puerto Limon, in Costa Rica, 20 Mart. 1930.

Caulerpa Vickersiae (originally *C. Vickersii*) as recognized by Børgesen (1) is a much larger plant than that described here. The forking of ramuli is not unknown in the species, but here it is so pronounced as to be the most striking character of the plant, and, combined with a departure from the typical distichous arrangement of the ramuli in their assumption of a generally radial position, effectively characterizes the variety. The axes of the

new variety, both repent and erect, are more slender, and the ramuli are more slender and also shorter. The variety *furcifolia* contrasts sharply with, and is opposite in its trend of development from, the variety *luxurians* from Florida described by the writer (3). These varieties, not readily accommodated within the typical species concept, are so obviously related to it that their recognition and description as varieties seem to be the best way of designating the broadening concept of *C. Vickersiae*, and the most in accord with current practice in this involved genus.

In Figure 1 there is illustrated a considerable fraction of a plant which has been selected because it showed in some portions distinct evidence of the pinnate disposition of the ramuli characteristic of the typical form. Some branches reveal little trace of the varietal peculiarities other than size and proportions; in general it is not representative of the bulk of the material, but is, rather, an important connecting link. In Figure 2 there is represented a more characteristic branch, with the ramuli, mostly forked, radially disposed throughout. They have the maximum of length and the minimum of forking. The condition in Figure 3 is more extreme, with the densely forked ramuli present on the midportion of the axis. Similar ramuli appear in some parts of Figure 1, and often complete systems of ramuli were thus clothed throughout. Such conditions were extremely hard to draw from the available dried material, since, on soaking, the thin-walled ramuli never entirely resumed their normal stature and position, and the specimens represented were not so elaborate as those which would have been selected from living or fluid-preserved material.

PHAEOPHYCEAE

Ectocarpus breviarticulatus J. Ag.

Neurocarpus delicatulus (Lamx.) Ktze.

Padina gymnospora (Kg.) Vick.

Spatoglossum Schroederi (Mart.) J. Ag.

Sargassum fluitans Børg.

RHODOPHYCEAE

Galaxaura elongata (E. & S.) Lamx.
Gelidium pusillum (Stackh.) Le Jolis.
Gelidium rigidum (Vahl) Grev.
Hypnea musciformis (Wulf.) Lamx.–(Rio Cienequita)
Hypnea spinella (C. Ag.) Kg.
Agardhiella tenera (J. Ag.) Schm.
Chrysymenia uvaria (L.) Le Jolis.
Acanthophora muscoides (L.) Bory.
Laurencia intricata Lamx.
Laurencia microcladia Kg.
Laurencia papillosa (Forsk.) Grev.
Laurencia scoparia J. Ag. (6).
Polysiphonia ferulacea Suhr.
Centroceras clavulatum (C. Ag.) Mont.
Ceramium subtile J. Ag.
Spyridia filamentosa (Wulf.) Harv.
Wrangelia Argus Mont.
Ochtodes secundiramea (Mert.) Howe.
Grateloupia dichotoma J. Ag.
Grateloupia filicina (Wulf.) J. Ag.
Peyssonnelia rubra (Grev.) J. Ag.
Amphiroa fragilissima (L.) Lamx.
Jania capillacea Harv.
Dermatolithon pustulatum (Lamx.) Fosl.
Goniolithon Boergesenii Fosl.
Melobesia farinosa Lamx.

Marine Algae from Jamaica

The marine flora of the large island of Jamaica was thoroughly reviewed by F. S. Collins in 1901 (2), and the list then published gave a comprehensive survey of the work previously done by various investigators. Since that time only a short note by the present writer (4) directly reports on a collection from the island, although Jamaican specimens are occasionally referred to in the literature. The late Mr. C. R. Orcutt made a collection of various plant groups, including algae, in the West Indies, and particularly in Jamaica. On his death the algae came into the hands of the present writer for study, through the kindness of Mr. Wm. R. Maxon of the United States National Herbarium, to which institution the first set of the material has been returned for deposit. Because

of the fact that very many of the collection numbers contained more than one item, it is difficult to indicate the quantity of material and the data secured; in brief, it may be said that about eighty species of marine algae were in a state enabling a satisfactory determination to be made. No attempt was made to search for microscopic forms, or to study the fresh-water material.

Since the phycological flora of the sea about the island has already been somewhat studied, it is not surprising, in the light of the Orcutt collection, that but few additions are to be made to the list. The following are believed to be new records for the island; new stations for plants already reported are not listed here.

MYXOPHYCEAE

Hydrocoleum comoides Gom. Abingdon.

CHLOROPHYCEAE

Enteromorpha lingulata J. Ag. Palisadoes at Port Royal; Port Henderson.

Cladophoropsis macromeres Taylor. Abingdon.

Codium isthmocladum Vickers. Harbor Head; Port Royal.

Halimeda Opuntia var. triloba (Decne.) Bart. Robins Bay

PHAEOPHYCEAE

Ectocarpus Duchassaignianus Grun. Harbor Head.

RHODOPHYCEAE

Erythrocladia subintegra Rosenv. On Amphibia, Green Island wharf.

Wurdemannia setacea Harv. Kingston.

Hypnea cervicornis J. Ag. Runaway Bay; Abingdon.

Polysiphonia subtilissima Mont. Green Island; Rockfort; Kingston.

Amphiroa Tribulus (E. & S.) Sol. Robins Bay.

Jania adherens Lamx. Robins Bay; Harboreale. December.

Marine Algae from Hispaniola

Some time since, the writer had occasion to examine certain series of specimens of marine algae from the Republic of Haiti on the island of Hispaniola; he reported on them in conjunction with Dr. C. H. Arndt, the collector (5). Since Dr. Arndt's stay on the island lasted for but a short time beyond the appearance of the joint paper, it was possible for him to extend his collecting in only a few directions, but the results of certain trips in 1929 were obligingly made available to the writer late in that year. Through the kindness of Mr. Maxon a considerably larger bulk of Haitian material, collected by Mr. Orcutt, has also reached his hands. Together they effect a very considerable addition to the recorded flora, which with the increase here made amounts to some one hundred and sixty species, with sundry varieties and forms.

The Arndt stations for the material of this paper include Port-au-Prince, Petit Goave, Miragoane, and Aquin, places on or at the base of the southwestern peninsula and mostly near the eastern portions of the north and south shores. In addition, an important group of specimens came from Cap Haitien on the north shore of the main island. So far as they are available, descriptions of these stations have been given (5). A few notes on seasonal abundance are incorporated in the list of species.

Most of the Orcutt collections were made farther to the west (July–August 1929), on the extreme southwestern and western limits of the peninsula, including Anse d'Hainault, Damassin, Coteaux, Roche à Bateaux, Anse à Drick, Port Salut, St. Jean du Sud, Torbeck, Cayes, and the Ile à Vache, with some minor stations which to the present have proved impossible to locate exactly on the map. Most of the material came from Port Salut and Torbeck. No details of habitat are available for any of these stations.

Listing only those species for which the range on the island must be extended, we have the following:

MYXOPHYCEAE

LYNGBYA CONFERVOIDES C. Ag. ex Gom. Coteaux. July?

LYNGBYA MAJUSCULA Harv. ex. Gom. Torbeck River; Cap Haitien. July, August.

LYNGBYA SEMIPLENA J. Ag. ex Gom. Miragoane Bay. February.

LYNGBYA WILLEI Setch. & Gardn. With *L. semiplena*, Miragoane Bay. February.

MICROCOLEUS CHTHONOPLASTES (Fl. Dan.) Thuret ex Gom. Baraderes Bay. February.

HORMOTHAMNION ENTEROMORPHOIDES Grun. Petit Goave. August.

RIVULARIA BIASOLETTIANA Menegh. ex Born. & Flah. Petit Goave. October.

RIVULARIA POLYOTIS (C. Ag.) Born. & Flah. Petit Goave. August.

CHLOROPHYCEAE

ENTEROMORPHA CLATHRATA (Roth) Grev. Coteaux. July.

ENTEROMORPHA LINGULATA J. Ag. Coteaux; Port Salut. July.

ENTEROMORPHA TORTA Reinb. Miragoane Bay. February.

ULVA LACTUCA L. Petit Goave. June.

ULVA LACTUCA var. RIGIDA (C. Ag.) Le Jolis. Roche à Bateaux. July.

PROTODERMA MARINUM Hauck. With *Rivularia Biasolettiana*, Petit Goave. October.

CHAETOMORPHA CLAVATA (C. Ag.) Kg. Port Salut. July.

CHAETOMORPHA GRACILIS Kg. Port Salut. July.

CLADOPHORA FASCICULARIS (Mert.) Kg. Damassin; Port Salut; Torbeck. July.

CLADOPHORA FULIGINOSA Kg. Cap Haitien. August.

CLADOPHORA GLAUCESCENS (Griff.) Harv. Port Salut. July.

CLADOPHOROPSIS MEMBRANACEA (C. Ag.) Børg. Miragoane Bay; Port Salut. October.

ANADYOMENE STELLATA (Wulf.) Harv. Petit Goave; Damassin; Roche à Bateaux; Port Salut. July.

CHAMAEDORIS PENICULUM (Sol.) Ktze. Foux Cap. August.

Dictyosphaeria favulosa (C. Ag.) Decne. Cap Haitien; Point Sable. August.

? Valonia pachynema (Harv.) Mart. Anse d'Hainault; Foux Cap. August.

Valonia ventricosa J. Ag. Point Sable.

Acetabulum crenulatum (Lamx.) Ktze. Port Salut.

Cymopolia barbata Lamx. Ile à Vache. June.

Dasycladus vermicularis (Scop.) Kras. Aquin. November.

Bryopsis Duchassaignii J. Ag. Port Salut. July.

Caulerpa fastigiata Mont. Miragoane Bay. October.

Caulerpa racemosa (Forsk.) J. Ag. Miragoane Bay; Ile à Vache. October; June.

Caulerpa sertularioides (Gmel.) Howe. Port Salut. July.

Avrainvillea Rawsoni (Dickie) Howe. Roche à Bateaux. July.

Codium intertextum Collins & Hervey. Coteaux. July.

Codium isthmocladum Vickers. Ile à Vache. June.

Penicillus capitatus Lamx. Cap Haitien; Port Salut; Roche à Bateaux. August.

Rhipocephalus Phoenix (E. & S.) Kg. Anse d'Hainault. August.

Udotea Flabellum (E. & S.) Howe. Point Sable.

Caulerpas and Halimedas were more abundant at Petit Goave Beach in the spring of 1929, according to reports from Dr. Arndt, than in the autumn; *Enteromorpha flexuosa* was common at the same station in January, but sparse in August and October of the same year.

PHAEOPHYCEAE

Dictyota Bartayresii Lamx. Port Salut; Aquin. November.

Dictyota cervicornis Kg. Cap Haitien; Petit Goave; Port Salut. August.

Dictyota ciliolata Kg. Cap Haitien; Aquin. August; November.

Dictyota dentata Lamx. Cap Haitien. August.

Dictyota pardalis Kg. Ile à Vache. June.

Dilophus guineensis (Kg.) J. Ag. Petit Goave. June.

Neurocarpus delicatulus (Lamx.) Ktze. (= *N. Hauckianus* (Möb.) Kg.). Cap Haitien. August.

Neurocarpus Justii (Lamx.) Ktze. East of Port Salut. July.

Zonaria variegata (Lamx.) Mert. Torbeck; Aquin; Foux Cap. August.

Zonaria zonalis (Lamx.) Howe. Petit Goave; Roche à Bateaux; Torbeck. July.

Sargassum filipendula C. Ag. Near St. Jean du Sud. July.

Sargassum polyceratium var. ovatum (Collins) Taylor. Cap Haitien. August.

RHODOPHYCEAE

Bangiopsis subsimplex (Mont.) Schm. Port Salut. July.

Liagora ceranoides Lamx. Coteaux; near Caspentia. July.

Liagora farinosa Lamx. Near Caspentia.

Galaxaura cylindrica (Sol.) Lamx. Torbeck.

Galaxaura marginata (E. & S.) Lamx. Roche à Bateaux.

Galaxaura oblongata (E. & S.) Lamx. Cap Haitien; Petit Goave; Ile à Vache; Point Sable. August; July; June.

Galaxaura obtusata (E. & S.) Lamx. Coteaux. July.

Galaxaura rugosa (Sol.) Lamx. Port Salut. July.

Galaxaura squalida Kjellm. Cap Haitien; Port Salut; Ile à Vache; Foux Cap.

Gelidium crinale (Turn.) Lamx. Torbeck.

Wurdemannia setacea Harv. Roche à Bateaux; Port Salut. July.

Agardhiella tenera (J. Ag.) Schm. Anse à Drick; Point Sable.

Eucheuma isiforme (C. Ag.) J. Ag. Foux Cap. August.

Gracilaria Blodgettii Harv. Aquin.

Gracilaria cervicornis (Turn.) J. Ag. (= *G. domingensis* Sond. *sensu* Collins). Coteaux.

Gracilaria confervoides (L.) Grev. Petit Goave; Aquin.

Gracilaria cornea (Turn.) J. Ag. Torbeck.

Gracilaria crassissima Crn. Ile à Vache. June.

Gracilaria ferox J. Ag. Cap Haitien. August.

Hypnea cervicornis J. Ag. Cap Haitien; Aquin. August; November.

Hypnea cornuta (Lamx.) J. Ag. Cap Haitien.

Hypnea musciformis (Wulf.) Lamx. Roche à Bateaux; Port Salut. July.
Hypnea spinella (C. Ag.) Kg. Point Sable.
Champia parvula (C. Ag.) Harv. Port-au-Prince Bay; Petit Goave; Point Sable. June, August.
Coelothrix irregularis (Harv.) Børg. Roche à Bateaux. July.
Ancanthophora muscoides (L.) Bory. Torbeck; Port Salut.
Amphibia tenella (Vahl) Ktze. Port Salut.
Bryothamnion triquetrum (Gmel.) Howe. Point Sable.
Chondria atropurpurea Harv. Port Salut.
Chondria littoralis Harv. Port Salut. July.
Chondria tenuissima (G. & W.) C. Ag. Roche à Bateaux. July.
Dasya corymbifera J. Ag. Petit Goave.
Digenia simplex (Wulf.) C. Ag. Port Salut.
Heterosiphonia Wurdemanni (Bail.) Falk. Aquin.
Laurencia microcladia Kg. Cap Haitien; Petit Goave.
Lophosiphonia obscura Auct. Port Salut; Aquin.
Polysiphonia ferulacea Suhr. Torbeck. July.
Centroceras clavulatum (C. Ag.) Mont. Torbeck; Port Salut.
Ceramium nitens (C. Ag.) J. Ag. Anse d'Hainault; Port Salut; Aquin. August.
Ceramium subtile J. Ag. Coteaux.
Spyridia clavata Kg. Port Salut. July.
Spyridia filamentosa (Wulf.) Harv. Port Salut. July.
Grateloupia filicina (Wulf.) Ag. Damassin; Port Salut; near St. Jean du Sud; Torbeck. July.
Halymenia Floresia (Clem.) J. Ag. Torbeck.
Ochtodes secundiramea (Mont.) Howe. Foux Cap. August.
Peyssonnelia rubra (Grev.) J. Ag. Cap Haitien; Point Sable.
Amphiroa fragilissima (L.) Lamx. Coteaux.
Corallina cubensis Mont. Point Sable.
Corallina subulata E. & S. Point Sable.
Jania adherens Lamx. Port Salut; Point Sable.
Jania capillacea Harv. Petit Goave; Port Salut; Point Sable.
Jania pumila Lamx. Roche à Bateaux. July.
Goniolithon Boergesenii Fosl. Petit Goave. October.

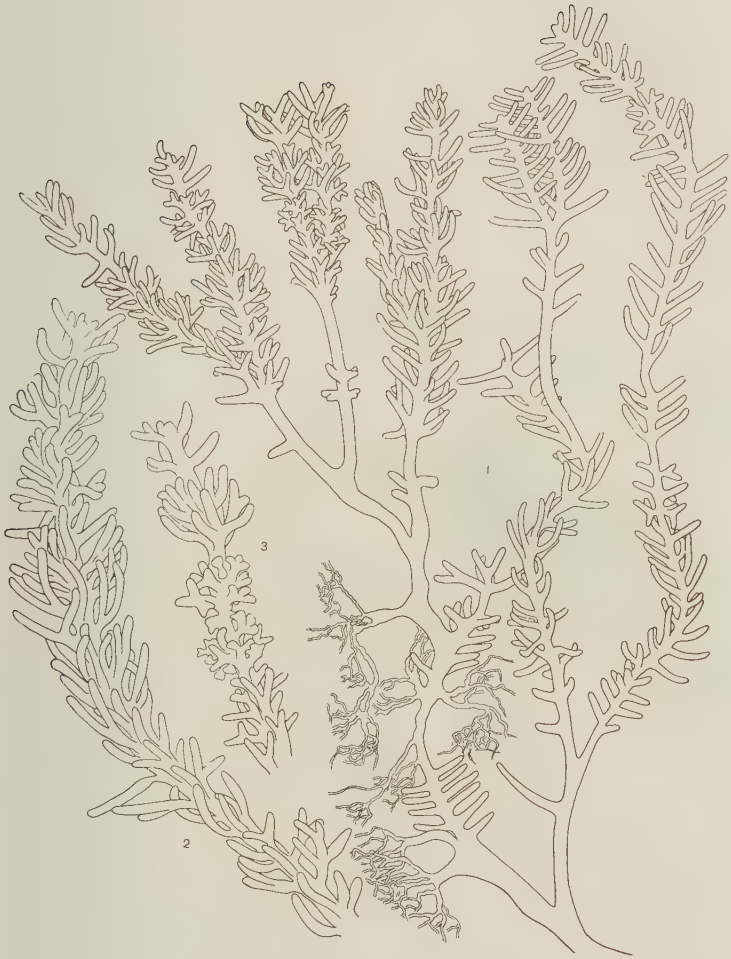
Goniolithon solubile Fosl. & Howe. Aquin. November.
Lithophyllum caribaeum Fosl. Aquin Bay. November.
Melobesia bermudensis Fosl. Aquin Bay. November.
Melobesia farinosa Lamx. Point Sable.
Melobesia farinosa var. Solmsiana (Falk.) Lem. Point Sable.

Certain variation in abundance of Rhodophyceae, as well as of Chlorophyceae, appears to have occurred at Petit Goave Beach. Among plants which seem to have been more abundant in the spring than in the autumn are *Acanthophora spicifera*, *Coelothrix irregularis*, *Digenia simplex*, *Spyridia aculeata*, and *Liagora sps.* Acanthophora, Spyridia, and Coelothrix seemed to decrease in abundance in the early autumn; Liagora and Digenia even earlier. In January Acanthophora, Liagora, and Digenia were already abundant, but the others seemed to develop later. Since the observations were made in only one year they may not represent a repeating cycle.

In the earlier paper (5) it was suggested that the small apparent differences between the floras of the north and south shores of the peninsula would disappear as fuller information became available. This is not yet true. Of the eight species mentioned as limited to the north shore, three (*Cladophora fascicularis*, *Dictyota Bartayresii*, and *Centroceras clavulatum*) are now known from the south shore, and *Jania capillacea* appears on the north side. However, with the growing list and a shift in attention to south-coast ports, we have an increase rather than a decrease in the species of limited known distribution, so that approximately forty-four plants are known from the north shore only, fifty from the south shore only, and fifty-seven are shared in common; additional records from Cap Haitien, Point Sable, and Foux Cap are disregarded. Some specialized habitats, such as that of Baraderes Bay, account for a number of species in their limited range; the rest will be cleared up only by a thorough field study.

University of Michigan

PLATE XXXVI



Caulerpa Vickersiae var. *furcifolia*, var. nov.

FIG. 1. Portion of plant showing rhizomatous axis, rhizoidal branches, and foliar branches, which exhibit transitions from pinnate to radial disposition of the ramuli and from simple to repeatedly forked ramuli. × 12

FIGS. 2–3. Branches with increasing degrees of ramular forking and condensation. × 25

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SOME RELATIONSHIPS BETWEEN WATER PLANTS AND WATER SOILS IN MICHIGAN

JETHRO OTTO VEATCH

THE water-covered surfaces of the earth have been studied by geologists and physiographers, and a very considerable literature has been accumulated on the origin of the features and the phenomena of sedimentation. Limnologists have conducted extensive studies on the biology of the waters and sediments, particularly at the greater depths, and on the temperature and the gaseous content of the waters. A comprehensive paper of a limnological and geological nature summarizing the literature has recently been published by Dr. E. Wasmund.[1] Botanists have identified the species of aquatic, or hydrophytic, plants throughout the world, and evidently many papers are available on the anatomy, physiology, life-history, and ecology of this group of plants.[2] Chemists, also, have made innumerable analyses of surface waters. Lake surveys, showing depths, kinds of bottom, vegetation, and shore lines in relation to use of the waters for propagation of fish and for recreational purposes, have been made. Water-covered areas, however, have received very little attention from a purely pedologic point of view, although there are a few references in German literature, and the author of this paper recently proposed a tentative classification of water soils in Michigan.[3]

The pedologic studies which the author has made in Michigan

[1] Wasmund, E., "Lakustrische Unterwasserboden," *Handbuch der Bodenlehre,* Fünfter Band, herausgegeben von Dr. E. Blanck, pp. 97–161 (Verlag von Julius Springer, Berlin, 1930).

[2] Reference is made especially to the monograph and bibliography by Arber, Agnes, *Water Plants* (Cambridge University Press, London, 1920).

[3] Veatch, J. O., "Classification of Water Soils," *Quarterly Bulletin,* 14, No. 1, Michigan Agricultural Experiment Station, August, 1931.

have been restricted very largely to inland lakes, although some observations were made on marshes and streams. Further, the studies were confined to a group, or order, based on depth of the aqueous horizon, to about ten feet, which might be designated as the "littoral" or the "epilimnion"; the waters are all relatively clear, and all non-saline, and all in the calcareous group, though this group is characterized by a wide range in the amount of matter in solution. The conditions in the aqueous horizon which were considered of most pedologic significance and value as criteria in differentiation of the particular group defined are: (1) range in hardness (since this is the most practicable means of comparing the amounts of bicarbonates of calcium and magnesium in solution); (2) reaction or pH; (3) thickness or depth. The subaqueous, cumulose horizon and the substratum were subdivided according to the texture, consistency, and composition, whether mainly organic or inorganic. Thus the principal types were: (1) sand-gravel-cobble; (2) medium and fine sand; (3) peaty sand; (4) mud, or clay, inorganic; (5) the fine, slimy fluid peat; (6) the coarse, or compact and fibrous, peat; (7) the pure marl or calcareous mud; (8) the calcareous peat or peaty marl; (9) the coarse pebbly or sandy marl; (10) the hard or indurated rock bottom. The thickness of the cumulose horizon is obviously important.

Only a few chemical analyses were made, but these were sufficient to indicate that the types of bottom enumerated differ considerably in the amounts of the nutrient elements such as nitrogen, phosphorus, calcium, and potassium. Determinations were also made on the pH and the hardness of the waters. A range from about 6 to 9.2 pH was found, and a hardness of 1.5 to 20 expressed as grains per U. S. gallon.

Observations on aquatic plants were made as the water soil type was determined in order to ascertain whether any significant ecologic relationships might exist. No attempt was made, however, to carry on quantitative studies. The observations were extensive and of a reconnaissance nature; the conclusions presented should be judged accordingly. About three hundred separate localities widely distributed over the state were visited in order to include

all the major physiographic and geologic conditions. At each locality notes were made on the apparent abundance or paucity of growth; on the nature of the plant association according to the apparent dominance of any one genus or according to diversity of species; and on a few easily recognized species and genera, with the purpose in mind of determining the range in natural conditions under which they grow.

The general conclusions, after a study of the tabulated observations, are given here. In relation to the kind of bottom, or cumulose horizon, the most prolific growth of attached plants appears on the soft, slimy sedimentary peat, or organic mud; or upon the soft silty or clayey inorganic muds. The least growth appears on the nearly pure sand, cobbles, and hard rock. In relation to the amount of lime in the water, expressed as hardness, the more calcareous water appears to support a denser growth than the soft water, especially where the latter is dark-colored from dissolved or suspended organic compounds. In relation to the reaction of the bottom, or subaqueous, soil in marshes and bogs, a marked difference appears in the composition of the vegetation. In lakes where the waters were nearly neutral, and slightly acid, there is a difference in the relative abundance of separate species as compared with the markedly alkaline waters, but apparently there is no complete inhibiting effect on the growth of the plants common in alkaline water until the lake basin is almost entirely occupied by the acid bog type of vegetation, characterized by leatherleaf, cranberry, blueberry, cotton grass, sphagnum, etc.

There are some species, of Chara, for example, which may be definitely limited by the amount of calcium in the water and soil, but the conclusion was reached that most of the aquatic plants observed grow under a comparatively wide range of soil conditions. It is reasonable to assume, however, that there is an optimum soil condition for every species.

The observations made support a theory that many of the present acid and soft-water lakes and bogs were originally alkaline and hard-water lakes, and that the change from one condition to the other has resulted from filling by vegetation to such a point that some part of the basin has only a very small depth of water

covering it. When this stage is reached, acid-tolerant plants, such as leatherleaf (*Chamaedaphne calyculata*), establish themselves and gradually crowd out the original calciphile plants. In such cases deep open water may remain alkaline and hard until completely surrounded by the acid bog vegetation. There may be observed in various stages of change water and plant associations which result in curious mixtures of commonly acid and commonly calcareous vegetation, the latter either having adjusted itself to the new environment or being in the process of extinction. In many basins there is a distinct zonation according to the kind of subaqueous soil and water, but with a blending of one zone into another. Photographs illustrating the evolution from the open alkaline water stage to the nearly completely filled acid bog and the mixture of acid and calcareous vegetation are shown in Plates XXXVII–XXXVIII. Considering the geological associations of some of the very soft-water lakes and acid bogs and swamps, it seems almost inconceivable that the original open water of the lake basin was other than highly charged with calcium bicarbonate. The associated surface formations of glacial origin may be highly calcareous, and well water from the older formations show a high degree of hardness, but, notwithstanding, soft-water lakes and acid bogs exist. There is some evidence that a "softening" process takes place in lakes in which vegetation has accumulated, since in a number of instances the inflowing stream and spring waters were harder and more alkaline that that of the lake.

Observations on the nature of the habitat of a number of aquatic plants are here given.

The genus Potamogeton is widely distributed throughout the state, without exception as to geographic or physiographic division. The growth appears to be most prolific in the calcareous and alkaline waters and on the soft or fluid organic "mud," and on the soft marl. Some of the species, however, were observed on all types of bottom except indurated rock. One species (*P. filiformis ?*) was noted as being common in very soft or even slightly acid water.

The water lilies (Nymphaea and Castalia) appeared to be most abundant in soft, fluid, organic mud, in waters with a range

FIG. 1. Border of acid peat, supporting leatherleaf and black spruce. Early stage in conversion of alkaline water to acid water and acid type of vegetation. East Lake, Kalkaska County, Michigan

FIG. 2. Small patch of leatherleaf and other acid bog plants appearing in the center (near fence) of a lake completely filled with vegetation, which is predominantly non-acid. Near Manchester, Washtenaw County, Michigan

FIG. 1. Lake basin nearly completely filled with acid peat and having only a very narrow outer zone of cat-tail and other non-acid vegetation remaining. Near Highland, Oakland County, Michigan

FIG. 2. Encroachment of acid vegetation, indicated by shrub leatherleaf, on non-acid and open-water vegetation (in the foreground) such as Pontederia, Sagittaria, Nymphaea, and Brasenia. Strewin Lake, Barry County, Michigan

of hardness of 5 to 20 grains per gallon, but a number of instances were recorded in which they appeared in very soft and even slightly acid water and acid peaty mud.

Scirpus validus, and possibly closely related species, was noted as being common on "hard" bottoms, except hard bedrock, regardless of the texture and composition, and in alkaline and hard water, but there are several records in which it appeared in slightly acid water and on coarse and compact acid peat.

Wild rice (*Zizania aquatica*) in five localities grew in clear water, with a range of hardness of 6 to 17 grains per gallon, a pH of 8.0 to 8.6; the bottoms were soft, fluid, organic mud or peat, thin peaty mud over calcareous clay, and clayey, inorganic, calcareous mud.

Sagittaria and Pontederia appeared to be most prolific in shallow alkaline or hard water over the more clayey (inorganic) mud or in peaty sands, but a few were recorded on acid peats.

Cat-tail (*Typha latifolia*) occurred under a wide range of soil conditions, but showed the heaviest growth on the more clayey muds and on a thin covering of black alkaline muck over clay or calcareous sand and silt; the associated water was alkaline in reaction. Cat-tails were observed, however, on strongly acid, coarse peat, but were not abundant.

Chara showed a wide range in the kind of bottom, but was most abundant where a soft calcareous mud or ooze was present. There was no instance of its occurrence in water having fewer than 6 grains per gallon of hardness.

Eriocaulon septangulare appeared to be a very reliable indicator of soft, and nearly neutral or slightly acid, water, of small depth, over either peat, peaty sand, or clean non-calcareous sand.

Michigan State College
East Lansing, Michigan

SEED STUDIES IN *CYCLAMEN PERSICUM* MILL

EDWARD F. WOODCOCK

THE earlier investigators of seed morphology found the curved embryo of so common occurrence in certain groups of plants that Engler and Prantl (2) felt justified in placing them in the order Caryophyllales or Curvembryoneae. The results of serum diagnosis by Malligson (4) show not only a close relationship between the members of Caryophyllales, but also the fact that the order Primulales is closely related to the order Caryophyllales.

The results of recent investigations on the seed morphology of Caryophyllales by Stevens (5), Artschwager (1), and the writer (6–15) also indicate that a close relationship exists in the order. Table I summarizes the information obtained by these investigators concerning the seed morphology.

The close relationship of Primulales and Caryophyllales, discovered by Malligson, suggested to the writer a study of the seed morphology of the order Primulales. *Cyclamen persicum* Mill. was selected as a representative; this paper deals with all the stages of seed development. The early stages were studied by means of microtome sections stained with Delafield's hematoxylon. Gressner (3) has reported concerning the germination of Cyclamen seeds, but not concerning the early stages of seed development.

DESCRIPTION AND DISCUSSION OF THE MORPHOLOGY OF THE SEED

The compound pistil has free central placenta and the campylotropous ovules are somewhat imbedded in the placental tissue. The young, unfertilized ovule is slightly elongated and circular in cross-section (Pl. XXXIX, Fig. 1). The ovules are so small and irregularly arranged that the writer found it almost impossible to get good median longitudinal sections.

TABLE I

SEED CHARACTERISTICS IN THE CARYOPHYLLALES

The shape of the embryo in each family is curved.

Family	Endosperm	Perisperm
Polygonaceae	Present	Absent
Chenopodiaceae	Present only as cap over tip of radicle	Present
Aizoaceae	do.	Present
Nyctaginaceae	Absent	Present
Phytolaccaceae	Present only as cap over tip of radicle	Present
Cynocrambaceae	Present	Absent
Caryophyllaceae	Present only as cap over tip of radicle	Present
Portulacaceae	Compressed sheath of empty cells about embryo	Present
Amaranthaceae	Present only as a cap over tip of radicle	Present

There is only one integument, and it is composed of two layers of cells. The cells are not flattened as is usually the case in most plants. The micropylar portion of the integument is somewhat thickened. There is no evidence of an integument below the micropyle, and the nucellus tissue apparently extends to the surface of the ovule. The cells of the nucellus opposite the micropyle are somewhat elongated and thus, perhaps, can better assist in the passage of the pollen tube from the micropyle to the embryo sac.

While the ovule is still young, the embryo sac enlarges very rapidly at the expense of the nucellus tissue. The free nuclear endosperm, developed as a result of fertilization, increases rapidly and soon forms a several-celled layer in contact with the embryo-sac wall (Fig. 3). Some very interesting changes occur in the structure of the integument during this endosperm development. The outer tangential wall of each of the cells of the outer layer of the integument increases in extent and becomes convex, thus

forming a papilla-like outgrowth. The cells of the inner layer of the integument increase radially until they are three or four times longer than broad. The protoplasm becomes denser, and a few new cell divisions occur (Fig. 2). The nucellus at this stage is represented by a layer of somewhat crushed cells, and the endosperm cells, except those in contact with the nucellus, are much vacuolated. The latter cells have more protoplasm and undergo cell division as further endosperm formation takes place.

As growth proceeds the nucellus continues to decrease in extent and the embryo sac becomes completely filled with cellular endosperms. While this rapid endosperm development occurs, the fertilized egg becomes differentiated into a short suspensor and embryo (Fig. 4). The suspensor consists of a few broad, cylindrical cells, and the embryo is differentiated into dermatogen, periblem, and plerome. The inner tangential walls and the inner portion of the radial walls of the inner layer of the integument become thickened, as shown in Figure 4. Dense protoplasm still fills the cell cavity while these cell-wall changes occur. The convex cell wall of the outer layer of integument cells is somewhat thickened and cutinized at this stage, and the cell cavity is filled with dense, brownish material.

As embryo development proceeds it shows a method of growth very unusual for a dicotyledonous plant. Only one cotyledonary zone of growth appears in the apical portion of the embryo. The other zone is represented by a prominent elevation, which undergoes no further changes as development continues (Pl. XL, Fig. 7). This atypical development of the cotyledons causes the radical and hypocotyl of the young embryo to be much thicker than the single cotyledon. The plumule region is indicated only by the procambium strand extending to the depression at the base of the developing cotyledon. As the embryo increases in length, the adjacent cellular endosperm becomes disorganized, thus permitting the enlargement of the embryo. The developing embryo does not always occupy the same relative position in the endosperm, as is shown by dissection of numerous seeds.

The brownish black mature seed (Fig. 8) presents some charac-

ters which are very different from those summarized in Table I. As a result of the crowding of the seeds on the free central placenta and their imbedded location, many of them are somewhat compressed and angular. The testa is relatively thin in contrast to the size of the seed, and the inner tangential and radial walls of the inner layer of the integument have increased in thickness to such an extent that the cell cavity is almost obliterated. Gressner observed a crystal of calcium oxalate in each of these cells. The outer tangential walls of the cells of this layer and the walls of the outer layer have become only slightly thickened. The convex outer tangential walls of the outer layer of cells have become more cutinized. The cell walls of the endosperm tissue are thick and have numerous, broad, simple pits unevenly distributed. No chemical tests of these walls were made by the writer, but no doubt the wall thickening is a hemicullulose which represents a storage form of food. The cell contents consist of protoplasm with which particles of protein and oil are mixed. The cells of the outer portion of the endosperm (Pl. XL, Fig. 6) are radially elongated and do not have so many pits as do the cells of the inner portion. The latter cells (Fig. 5) are nearly isodiametric.

The slightly curved embryo of the mature seed is imbedded in the endosperm, and usually is separated from the testa by several endosperm cells. The position of the embryo varies, but in general it occupies the position shown in Figure 8. The embryo is so placed that the ventral surface of the single cotyledon is toward the center of the seed. The margins of the cotyledon have turned upward toward the axis of the embryo during development, so that it is trough-shaped (Fig. 9) and has the same width as the hypocotyl (Fig. 10). Gressner found that the developed cotyledon remains within the seed coat during the germination process and acts as an absorbing organ. The undeveloped cotyledon starts growth as the seedling appears and serves as the first leaf of the young plant.

SUMMARY AND CONCLUSIONS

The ovule of *Cyclamen persicum* Mill. is campylotropous and has only one integument. The slightly curved embryo is imbedded

in the thick-walled endosperm, and it has only one cotyledon. The second cotyledon remains undeveloped during seed formation.

The slightly curved embryo is an indication of some relationship between the orders Primulales and Caryophyllales, but the presence of storage material on the walls of the endosperm as well as in the cell lumen of Cyclamen is a marked difference from the conditions in the order Caryophyllales. Since the presence of a "monocotyledonous dicotyledon" has been observed in widely separated families by various investigators, no phylogenetic significance can be attached to its appearance in Cyclamen.

Michigan State College
East Lansing, Michigan

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EXPLANATION OF PLATES XXXIX–XL

Seed of *Cyclamen persicum* Mill

All figures drawn with aid of camera lucida. The following abbreviations are used: C, cotyledon; CH, chalaza; E, embryo; EN, endosperm; ES, embryo sac; F, funiculus; H, hypocotyl; IN, integument; M, micropyle; N, nucellus; P, plumule; PC, procambium; R, radicle; S, suspensor; T, testa; UC, undeveloped cotyledon.

PLATE XXXIX

Fig. 1. Longitudinal section of young ovule, showing the short funiculus, curved embryo sac, and single integument (× 207)

Fig. 2. Cross-section in detail, showing integument, nucellus, and endosperm (× 75)

Fig. 3. Longitudinal section of ovule, showing the large embryo sac lined with a layer of cellular endosperm (× 32)

Fig. 4. Cross-section, showing young embryo in longitudinal section, nucellus in crushed condition, and integument changes (× 75)

PLATE XL

Fig. 5. Section through centrally placed endosperm cell, showing the very thick wall and broad pits (× 430)

Fig. 6. Section through cells at periphery of endosperm tissue, showing their radially extended shape and broad pits (× 430)

Fig. 7. Longitudinal section of young embryo, showing its "monocotyledonous" nature (× 75)

Fig. 8. Longitudinal section of mature seed, showing testa, endosperm, and embryo (× 16)

Fig. 9. Cross-section through cotyledon of mature embryo (× 40)

Fig. 10. Cross-section through hypocotyl of mature embryo (× 40)

PLATE XXXIX

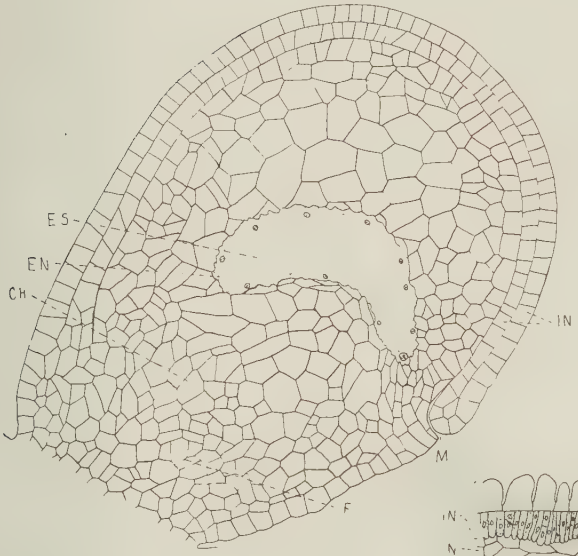

Fig 1

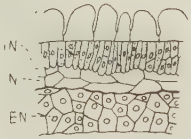

Fig 2

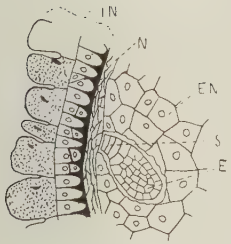

Fig 4

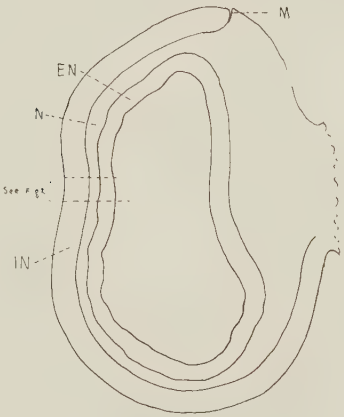

Fig 3

Seed of *Cyclamen persicum* Mill

PLATE XL

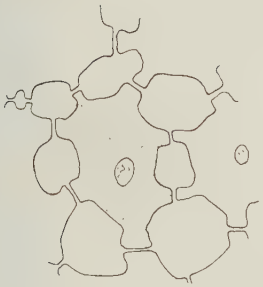

Fig. 5

Fig 6

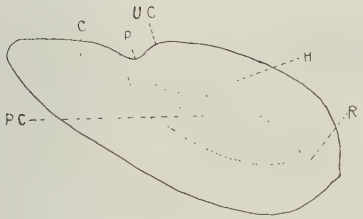

Fig 7

Fig. 9

Fig 10

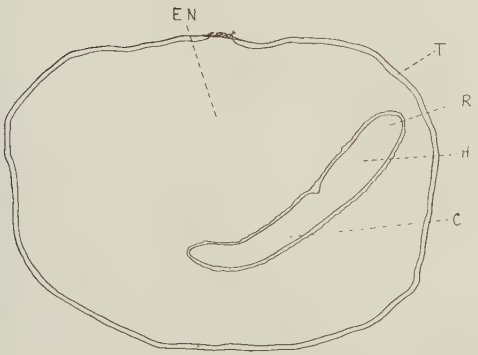

Fig. 8

Seed of *Cyclamen persicum* Mill

SOME RESUPINATE POLYPORES FROM THE REGION OF THE GREAT LAKES. IV *

DOW V. BAXTER

THE classification of many of the resupinate brown polypores has been a subject of interest among mycological students for years. Even so common and well known a plant as *Fomes igniarius* presents a perplexing problem for the student when this fungus appears in a resupinate form. In discussing the identity of resupinate forms of *F. igniarius* with the allied *Polyporus laevigatus*, for example, Lars Romell (20) states: "Though this species [*Pol. laevigatus*] is common at Stockholm where I have collected and studied it for more than twenty years, and though I have now compared it repeatedly with the resupinate specimens of *Pol. igniarius* from Lapland, and though some of them are tolerably alike, I am still in doubt as to whether their identity should be admitted or not."

Similar difficulties are encountered in the study of *F. igniarius* var. *nigricans*, *Poria betulina*, and other species. Preliminary investigations of several of these brown plants in culture indicate that characteristic growth forms develop and that these cultural characteristics may be employed to supplement the usual microscopic features in identification work. Marked differences in the growth of the mycelium of *F. igniarius* var. *nigricans*, *P. betulina*, *P. prunicola*, and *P. punctata* are pointed out in Table I and in Plates XLI and XLII. The characteristic habits of growth at different temperatures and on different media are evident and will be included in a later paper.

In this country a large number of porias have appeared in the literature. Since many plants were described from only a

* Contribution No. 34 from the School of Forestry and Conservation, University of Michigan.

TABLE I

GROWTH CHARACTERISTICS OF BROWN POLYPORES ON MALT AGAR

Name	In light				In dark			
	Rate in mm. 14 days	Color (Ridg.)	Texture	Agar discoloration	Rate in mm. 14 days	Color (Ridg.)	Texture	Agar discoloration
Fomes igniarius var. *nigricans* from *Betula alba*	20	Honey yellow to Verona brown	Arachnoid to slightly flaky	Deeply discolored under mycelium and at margin of culture	23	White to deep olive-buff	Arachnoid	Deeply discolored under mycelium and at margin of culture
Poria betulina from *Betula alba*	44	Clay color	Appressed	Slightly discolored in concentric rings	45	Tawny-olive	Granular to cottony	Deeply discolored in concentric rings
P. prunicola from *Prunus serotina*	16	Tawny-olive	Granular	Slightly discolored in concentric rings	23	White to chamois	Cottony	Deeply discolored in concentric rings
P. punctata from *Rhus vernix*	15	Cream-buff to chamois	Cottony	Not discolored	20	Cartridge-buff to chamois	Cottony	Not discolored

small amount of material or even from one collection, the limits of variation of some of these forms under different growing conditions and on the many possible different wood substrata are unknown. The lack of this knowledge undoubtedly has led to the description of several species which are actually conspecific with others. It should be pointed out, however, that a large number of the brown plants which are unknown plants to the region are chiefly tropical, and it is very unlikely that the majority of them will ever be found in the area of the Great Lakes.

In the third paper of this series a key was presented to the white, cinereous, yellow, and red resupinate polypores from the region of the Great Lakes (2). The continuation of this key in the present paper lists the brown resupinate plants which have been studied for the past several years. In addition to the numerous collections which have been made in this region and elsewhere, many herbarium specimens and types have been studied. Plants have been examined in the following institutions:[1] the University of Michigan, the University of Wisconsin, the Field Museum of Natural History, the New York State Museum, the New York Botanical Garden, the Division of Pathological Collections in Washington, and the Missouri Botanical Garden. Several collections have been studied at the Kew Gardens, Kew, England, and also in the herbaria at Uppsala and at the Riksmuseet Naturhistoriska, Stockholm.

[1] Throughout the course of this study I am indebted to many individuals for help in identifications and for specimens. I am under special obligation to Dr. L. O. Overholts, who identified many plants sent to him for study. Acknowledgment is due to Dr. James R. Weir and others who have expressed their opinion regarding the identity of certain collections. Thanks are also due to the authorities of the New York State Museum, the New York Botanical Garden, the Division of Pathological Collections in Washington, the Missouri Botanical Garden, the Field Museum of Natural History, the University of Wisconsin Herbarium, the Kew Herbarium, Kew Gardens, and to the herbaria at Uppsala and Stockholm in Sweden.

KEY TO THE PORIAS FROM THE REGION OF THE GREAT LAKES

(Continuation of the key which appeared in the third paper of this series [2] and which presented the white, cinereous, yellow, and red porias.)

Brown Plants

90. Setae absent 91
90. Setae present 103

91. On coniferous substratum 92
91. On hardwood substratum, also found on moss, stones, etc. 97

92. Plant fleshy, dingy whitish when fresh, becoming brown or brownish black when bruised or upon drying - when growing in partly illuminated and dark places (on foundation timbers in basements, etc.) surface frequently exhibiting distinct orange shades; pore mouths 1–3 to a mm., ranging up to 3 mm. long; spores dusky olive, 10–12 × 6–7.5 μ (Burt) (5)
P. incrassata (Berk. & Curt.) Burt
P. atrosporia Ames

92. Plant not fleshy when fresh, but leathery or woody, yellowish brown or brown at all times and not becoming black when bruised. Not commonly found on structural timbers 93

93. Plant exhibiting a dense, soft, feltlike subiculum over the surface of the substratum, even in dried specimens. Subiculose, sterile margin which surrounds the hymenium frequently several centimeters broad, "yellow ochre" and "antimony yellow" to "antique brown" (Ridg.); mouths 1–2 to a mm., "tawny-olive" (Ridg.); tubes up to 1.5 mm. long, mostly 1 mm.; spores 4–7 (7 × 4) 3–5 μ
P. subiculosa (Peck) Cooke
(Pl. XLIII)

93. Plant not exhibiting a dense, soft feltlike subiculum and wide feltlike margin, and not soft in the dried condition 94

94. Pore mouths 4–6 to a mm. (mostly 5-6); tubes 2–8 mm. long, mostly 4 mm. each season, becoming stratified — in old plants several centimeters thick; margin in old plants dark gray to black woody; spores globose 6–8 μ. On Tsuga, Abies, and other conifers
P. tsugina (Murr.) Sacc. & Trott.[2]
Fomes robustus Karst. (resupinate form)

[2] The characters of diagnostic value are the same in *P. tsugina* and *F. robustus*. The spore measurements are similar; the color and context seem to be the same. There are no setae in either plant. *P. tsugina* is found on conifers in the United States. A typical ungulate *F. robustus* on oak found in Stockholm, Sweden, is shown in Plate XLIV. *F. robustus* is reported on both hardwoods and conifers. A typical *P. tsugina* specimen from Wisconsin is illustrated in "Some Porias from the Region of the Great Lakes" (1).

94. Pore mouths 1–3 to a mm.; tubes usually not stratified, plants somewhat coriaceous — not woody and never several centimeters thick; spores cylindric to elongate-ellipsoid 95

95. Pore mouths hexagonal, regular, 1–3 to a mm.; tubes 1–3 mm. long. On charred wood ..... *P. carbonaria* Berk. & Curt.
Trametes sequoiae Copeland

95. Pore mouths daedaloid to labyrinthiform, irregular in size and shape, averaging 1–2 to a mm. On decorticated wood and occasionally on charred wood 96

96. Dissepiments of pores nearly 1 mm. thick; spores 8–12 × 3–5 μ (Shope). On decorticated and charred coniferous wood
Trametes odorata (Wulf.) Fr.
T. protracta Fr. ex Shope

96. Dissepiments of pores thin, of thickness of paper; spores 8–12 × 3–4.5 μ (Shope). Usually on hardwoods, but sometimes reported on conifers ..... *Lenzites trabea* (Pers.) Fr.[3]
L. vialis Peck ex Shope

97. Plant fleshy, dingy whitish when fresh, becoming brown or blackish when bruised or upon drying — when growing in partially illuminated and dark places (on foundation timbers in basements, etc.) surface frequently exhibiting distinct orange shades; pore mouths 1–3 to a mm., ranging up to 3 mm. long; spores dusky olive 10–12 × 6–7.5 μ. Usually on conifers, but the fungus is said to have the ability to attack practically all kinds of wood in the United States (7) ..... *P. incrassata* (Berk. & Curt.) Burt
P. atrospora Ames

97. Plant not fleshy at first, but coriaceous or woody; brown at all times 98

98. Plant sooty or brownish black; pore mouths 4–6 to a mm.; tubes 1–5 mm. long; spores 7 × 4.5 μ (Murr.) ..... *P. nigra Berk.*

98. Plant not sooty or blackish 99

99. Mouths daedaloid to labyrinthiform, irregular in size and shape and averaging 1–2 to a mm.; spores cylindric to elongate-ellipsoid, 8–12 × 3–4.5 μ (Shope). See No. 96 in key
Lenzites trabea (Pers.) Fr.
L. vialis Peck ex Shope [4]

99. Mouths distinctly poroid and regular, not daedaloid or labyrinthiform, averaging 3–8 (mostly 4–7) to a mm.; spores globose or subglobose 100

[3] This poroid form of a Lenzites is similar to *Lenzites saepiaria*, but the dissepiments of *L. saepiaria* are nearly 1 mm. thick. This distinction is held by Shope (22). Shope finds that *L. saepiaria* is lamellate from the very earliest stage, whereas *T. odorata* is never truly lamellate, although it may be labyrinthiform.

[4] See footnote to No. 96 in key.

100. Spores distinctly brown, 5–6 (5 × 4) 4 μ; tubes glistening, plant usually not more than 1 centimeter thick and mostly less; common on *Ilex verticellata* in the region of the Great Lakes and reported on Nemopanthus elsewhere (17) ..... *P. inermis* E. & E.

100. Spores mostly hyaline (pale ferruginous in *P. melleoporia*). Plant frequently several centimeters thick; not on Ilex and Nemopanthus 101

101. Spores 5–8, mostly 5–6 μ; pore mouths mostly 6–8 to a mm., "tawny-olive" or "Saccardo's umber" (Ridg.); tubes 1–3 mm. long each season, stuffed with gray mycelium, the tube layers reaching a thickness of more than 1 centimeter, surface very smooth, convex ..... *P. punctata* Fr.
P. laminata (Murr.) Sacc. & Trott.
P. obliquiformis (Murr.) Sacc. & Trott.
P. Friesiana Bres.

101. Spores 3–4 μ; pore mouths mostly 5–6 to a mm. 102

102. Plant coriaceous to rigid, tubes not whitish stuffed (Murr.); "Saccardo's umber" (Ridg.); not glistening-melleous; spores hyaline, 4 μ (Murr.) ..... *P. ohiensis* (Murr.) Sacc. & Trott.[5]

102. Plant rigid and woody, tubes whitish stuffed — at least in the old tube layers, flavous to melleous, mouths "buckthorn brown," subiculum darker, "Dresden brown" to "mummy brown" (Ridg.); spores brown 3–4 μ (Murr.)? (No spores to be found in cotype material of *P. Johnsoniana* from Ann Arbor)
P. melleoporia (Murr.) Sacc. & Trott.[6]
P. Johnsoniana (Murr.) Sacc. & Trott.

103. On coniferous substratum 104
103. On hardwood substratum 110

104. Pore mouths averaging 2–3 to a mm. 105
104. Pore mouths averaging 4–6 to a mm. 106

[5] Additional study may show that *P. ohiensis* may be conspecific with some other species. This plant has not been collected in the region of the Great Lakes, and the characters of diagnostic value have not been fully determined. Murrill (14) reports, "no cystidia, tubes 2-4 cm. long each season, not whitish stuffed."

[6] It is believed that there is no way to distinguish these two plants. Murrill gives the same spore measurements for the two plants, i.e. 3–4 μ. The distinguishing character used in his key calls for a difference in the thickness of the tubes in the two species. The tubes of *P. melleoporia* are said to be thin-walled, whereas those of *P. Johnsoniana* are thick-walled. I can see no appreciable difference in the walls of the two species. The name *P. melleoporia* is retained because it is more descriptive of the plant than is *P. Johnsoniana*. I cannot be certain about the spores being colored, since it is impossible to find any in the cotype collection of *P. Johnsoniana*.

105. Spores globose 4–5 μ (Shope) ..... *Trametes pini Abietis* Karst.
Polystictus piceinus (Peck) Sacc.

105. Spores cylindric or allantoid, but only slightly curved, 6–9 $\times$ 2 μ (Shope) ..... *Trametes isabellina* Fr.
T. tenuis Karst. ex Shope
T. setosus Weir ex Overh.
P. superficialis (Schw.) Cooke ex Overh.
P. viticola (Schw.) Cooke ex Overh.
P. contigua Karst. non *Pol. contiguus* of Fries ex Romell [7]

106. Each new stratum of the subiculum separated from the older one by a thin black layer which appears as a fine black line on a vertical section of the fungus, in most specimens to be seen only with the aid of a hand lens; tubes at length stratified, the strata separated from each other by a band of context about 1 mm. thick and exhibiting a thin black line or tube layers stratified without the "layers of context"; tubes 0.5–7 mm. long, mostly 6 mm. each season; pore mouths 4–6 to a mm.; cystidia 20–40 $\times$ 6–9 μ (Romell); spores 4–6 $\times$ 1.5–2 μ. Fungus causing a distinct white pocket rot in dead conifers. .... *F. nigrolimitatus* Romell (Pl. XLV)
Fomes putearius Weir ex Hubert [8]

106. Plant not stratified or, if stratified, each new stratum of the subiculum not separated from the older one by a thin black line; tubes never as long as 1 cm. and commonly averaging 2–4 mm. 107

107. Plant margin thick and frequently exhibiting a receding growth habit; tubes distinctly layered, walls of tubes exhibiting large brown hyphae which end as large protruding setae; spores ellipsoid, globose, or subglobose, hyaline 4–6 μ (Overh.). Fungus causes a separation of the annual layers in the wood — a ring scale rot on Thuja and an important fungus on *Thuja plicata*
P. Weirii (Murr.) Sacc. & Trott.

107. Plant margin not thick, and when mature frequently becoming entirely fertile; tubes seldom layered, and if so, indistinctly layered; plants not exhibiting receding growth habit. Fungus not characteristically causing a ring scale rot, and with the exception of No. 109, *P. ferruginosa*, commonly on substrata other than Thuja 108

[7] Romell (20) states: "*Pol. contiguus* of Fries is quite different according to the authentic specimens in his herbarium, two of which belong to *Pol. salicinus*, while the third is identical with *Pol. punctatus* (*Poria Friesiana* Bres.)."

[8] Overholts (18) reports that the spores of *Fomes putearius* are hyaline, globose, 4–5 $\times$ 3–4 μ (not colored, 7–8 μ). The spores of *F. nigrolimitatus* Romell are hyaline and cylindric. Romell's measurements for the spores of this plant are 4–6 $\times$ 1.5–2 μ (20). The two species are regarded as conspecific by Hubert (6).

108. Setae projecting, on the average, 25–60 μ (Overh.); pore mouths averaging not more than 4 to a mm., and usually 1–3; spores 6–9 $\times$ 2 μ (Shope) ..... *T. isabellina* Fr.
T. tenuis Karst ex Shope
T. setosus Weir ex Overh.
P. superficialis (Schw.) Cooke ex Overh.
P. viticola (Schw.) Cooke ex Overh.

108. Setae projecting, on the average, less than 35 μ; pore mouths averaging 4–6 to a mm. 109

109. Spores globose-ellipsoidal 4–5 (4 $\times$ 3) 2.5–4; tubes mostly 1–2 mm. long; plant margin usually not whitish in fresh plants. When found on conifers in the region, most commonly on Thuja but sometimes on Picea and Tsuga and other substrata
P. ferruginosa (Schrad.) Fr. (Pl. XLVI, Fig. 1)
P. macounii Peck [9]

109. Spores allantoid 3–5 $\times$ 1–2 (Overh.); tubes 2–4 mm.; long pore mouths "warm sepia," "cinnamon-brown," or "snuff brown" (Ridg.); margin whitish in fresh plants, becoming "Sudan brown," usually on spruce, fir, larch, or hemlock
P. ferrugineo-fusca Karst.
P. unita Fr. non Pers. ex Bres.
P. marginella Peck ex Bres., Overh., and others

110. Mouths greenish yellow when fresh, conspicuous, large, dark brown, thick-walled, hypha-like setae present in the trama; spores yellowish 4–5 (4 $\times$ 6) 5–6, usually growing under the bark of standing trees and sometimes under logs, the bark eventually falling away and exposing the fungus
Pol. glomeratus Peck (Pl. XLVI, Fig. 2, and Pl. XLVII)
P. Xanthospora Undw. ex Lloyd
P. Andersonii (E. & E.) Lloyd
P. setigera Peck? [10]

110. Mouths not greenish yellow when fresh, but brown or yellowish brown, reddish brown or some shade of brown; setal hyphae not conspicuous in the trama; spores hyaline or at least not distinctly yellowish. Plant usually not growing under the bark and especially under the bark of standing trees 111

111. Subiculum (context) yellow-brown 1–8 mm.; mouths of tubes exhibiting a distinct contrast in color to that of the subiculum, i.e.

[9] Overholts (15) finds that "the unusual habitat [creeping over and encrusting mosses] and the consequent irregularities of growth are the only separating characters" between *P. ferruginosa* and *P. macounii*.

[10] *P. setigera*, according to Overholts (18), is probably a young stage of *P. glomeratus*.

dark brown; spores 4–6 × 2.5–3.5 μ (Overh.). Plant usually effused-reflexed, not a true poria. ..... *Pol. gilvus* Schw. ex Fr.

111. Subiculum usually not yellow-brown but darker (and much less than 8 mm. in thickness); mouths of tubes usually not exhibiting a conspicuous contrast in color to that of the subiculum. Plant not reflexed (except *F. pomaceous*, *F. conchatus*, and occasionally *F. igniarius* var. *laevigatus*) 112

112. Spores definitely narrow and elongated, cylindric, 6–7.5 × 2–2.5 μ (Romell) (21) ..... *P. ferrea* Pers. ex Romell
Mucronoporus fulvidus E. & E. ex Overh.

112. Spores globose, subglobose, or oblong-ellipsoidal, less than 6 μ long and the length not two and one-half or three times their width ... 113

113. Plant woody (not coriaceous) and becoming definitely stratose, perennial 114

113. Plant not woody, but somewhat coriaceous; rarely stratose, and if so, very indistinctly; spores globose-ellipsoidal, 4–5 (4 × 3) 2.5–4; tubes mostly 1–2 mm. long ..... *P. ferruginosa* (Schrad.) Fr.
P. macounii Peck ? [11]

114. Cystidia or setae not brown, but appearing as projecting attenuate hyphae with an enlarged base; tubes soon whitish, stuffed; spores 5–8 μ. Plant never loosening from the substratum
P. punctata Fr.
P. laminata (Murr.) Sacc. & Trott.
P. obliquiformis (Murr.) Sacc. & Trott.
P. Friesiana Bres.

114. Setae brown 115

115. Growing on species of Prunus or Crataegus 116

115. Growing on other hardwood substrata 117

116. Margin circularly and obtusely ridged, becoming incrusted or horny; fungus causing a brown rot in species of Crataegus and Prunus; plant usually found on dead branches (Pl. XLVIII, Figs. 1–3) which cling to standing trees
Fomes pomaceus Pers. forma *Crataegi* [12]
F. fulvus Scopoli ex Bres. (resupinate form)

[11] See footnote to No. 109 in Key.

[12] The growth of this form on Crataegus has been followed for several years on trees in the vicinity of Ann Arbor. It retains the resupinate habit of growth. Many additional collections of this plant from Ann Arbor and elsewhere have been made. They exhibit setae. Since the fungus in question possesses the microscopic features of *F. pomaceus* and since the habit differences are not considered to be of specific rank, it is here treated as a form only.

The name *F. fulvus* appears extensively in the literature. Lloyd (9) states: "Persoon had a clear idea of *Fomes pomaceus*, as is evident from his specimen and writings, and he seems to have been the only one who had until recent years. Fries held it as a variety of *F. igniarius*, and his description of

116. Margin not circularly and obtusely ridged, not incrusted and horny. Fungus causing a white rot; in young stages fruiting structures first appear in circular patches, finally widely effused, their margins loosening naturally from the substratum in thin specimens; broadly ellipsoidal or subglobose 4–5 × 3–4 μ (Overh.). On logs and rarely on standing snags; cystidia 15–20 × 4–6 μ, basidia 4–6 μ in diameter (Overh.) ..... *P. prunicola* (Murr.) Sacc. & Trott. (Pl. XLIX and Pl. L, Fig. 1)

117. Plant conchate; margin with a sulcate brown or black surface; tubes 0.5–2 mm. long each season; pore mouths 4–6 to a mm.; spores subglobose 4–5 μ. Usually on black ash logs and standing snags of black ash in this region, but also found on other substrata *F. conchatus* Pers.[13]

117. Plant not conchate, margin not sulcate; usually on other substrata 118

118. Surface of pores brightly glistening, melleous, on oak, poplar, and various hardwoods 119

118. Surface of pores not brightly glistening or melleous, but frequently "velvety"; pore mouths averaging 4–6 to a mm.; spores hyaline 5–6.5 μ (Overh.). Plant frequently covering the entire under surface of logs. ..... *Fomes igniarius* var. *laevigatus*[14] Overh. (Pl. L, Fig. 2)

P. betulina (Murr.) Sacc. & Trott.

F. igniarius was drawn partially from this plant. Schroeter confused it with *F. igniarius*. Berkeley always referred it to *Fomes igniarius*. . . . Quélet got it right. Bresadola discovered that it was *Fomes fulvus* of Scopoli, being one of six different men who have interpreted Scopoli's vague writings, each one with a different species."

[13] Lloyd (9) lists two forms of *F. conchatus*, namely: "*F. salicinus* — Growing on willow, *Fomes conchatus* is usually subresupinate, or with a thick, imperfect pileate development. The context color is also darker. The microscopic features are the same. It is a host variation and difficult to clearly distinguish. The plant is more common on willow in Europe than in the United States. . . . *Fomes densus* — There occurs rarely in the United States and Europe a thick, heavy form of *F. conchatus*, differing only in not being thin." *Fomes densus* has been found on black ash in the Upper Peninsula of Michigan.

[14] *F. igniarius* is common on standing and fallen birches (as well as on other trees) in the region of the Great Lakes. In Sweden Romell (20) also finds it "on dead and fallen trunks of Betula through the whole birch region. . . . In Lappland this species occurs not only in the common ungulate form but also quite frequently in a more or less resupinate state. . . . Boudier's *Pol. nigricans* belongs here, and the form on Betula is Karsten's *Pol. nigricans*. Also Fries' original *Pol. nigricans* in *Syst. Myc.* I p. 375 is the Betula-form of *Polyp. igniarius* (Ad truncos Betulae, nec alibi). . . .

". . . If we admit the identity [of *Pol. laevigatus* and resupinate specimens of *Pol. igniarius*], the consequence seems to be that *P. laevigatus* is only

119. Margin of plant remaining attached to substratum inseparable, even after drying, usually glistening — "raw sienna"; pore mouths "antique brown" (Ridg.); tubes up to 4 mm. long, mostly 2.5 mm.; young mycelium in wood "mustard yellow" (Ridg.)
P. melleoporia (Murr.) Sacc. & Trott.
P. Johnsoniana (Murr.) Sacc. & Trott.

119. Margin of plant separating naturally from substratum, and especially when the plant is allowed to dry; margin "olive brown"; pore mouths "Saccardo's umber" to "olive-brown" (Ridg.); tubes mostly 6–10 mm. long. Young mycelium in wood "deep chrome" to "cadmium yellow" (Ridg.)
P. pereffusa (Murr.) Sacc. & Trott.? [15]

LIST OF BROWN RESUPINATE PLANTS FROM THE REGION OF THE GREAT LAKES

An asterisk (*) after a key number refers to a footnote; a dagger (†) indicates both text and footnote.

	Key No.
Fomes conchatus Pers.	117†
F. densus Lloyd	117*
F. fulvus Scopoli ex Bres. (resupinate form)	116†
F. igniarius Fr.	118*
F. igniarius var. laevigatus Overh.	118†
F. nigrolimitatus (Romell) Egeland	106†
F. pomaceus Pers. forma Crataegi	116†
F. putearius Weir ex Hubert	106†
F. robustus Karst. (resupinate form)	94*
Lenzites saepiaria (Wulf.) Fr.	96
L. trabea (Pers.) Fr.	99
L. vialis Peck ex Shope	96, 99
Mucronoporus fulvidus E. & E. ex Overh.	112
Polyporus gilvus Schw. ex Fr.	111
Pol. glomeratus Peck	110
Pol. laevigatus Fr.	118*
Pol. salicinus Fr.	105*
Polystictus piceinus (Peck) Sacc.	105
Poria Andersonii (E. & E.) Lloyd	110
P. atrospora Ames	92, 97
P. betulina (Murr.) Sacc. & Trott.	118
P. carbonaria Berk. & Curt.	95
P. contigua Karst. non Pol. contiguus of Fries ex Romell	105†
P. ferrea Pers. ex Romell	112
P. ferrugineo-fusca Karst.	109
P. ferruginosa (Schrad.) Fr.	109,† 113
P. Friesiana Bres.	101, 105,* 114
P. incrassata (Berk. & Curt.) Burt	93, 97

a form or variety of *P. igniarius*, and this can scarcely be conceded, as typical *P. laevigatus* appears quite distinct from typical *P. igniarius*.

"In *Pol. laevigatus*, which in its typical form is a thin, totally resupinate plant, the pores are small (5–7 or 4–8 mm.) with thin walls, while in *Pol. igniarius* the pores are a little larger (4–5 or 3–6 per mm.) with thicker walls. The spores of *Pol. laevigatus* are also small (3–5 μ diam. or 4–5 $\times$ 3–4 μ), while in *Pol. igniarius* the spores are larger (5–7.5 $\times$ 4–7 μ), but intermediate sizes are also noted. The hymenial spines are about the same in both species."

[15] Probably conspecific with other described species.

	Key No.
P. inermis E. & E.	100
P. Johnsoniana (Murr.) Sacc. & Trott.	102,† 119
P. laminata (Murr.) Sacc. & Trott.	101, 114
P. macounii Peck	109,† 113
P. marginella Peck ex Bres.	109
P. melleoporia (Murr.) Sacc. & Trott.	102,† 119
P. nigra Berk.	98
P. obliquiformis (Murr.) Sacc. & Trott.	101, 114
P. ohiensis (Murr.) Sacc. & Trott.	102†
P. pereffusa (Murr.) Sacc. & Trott.	119
P. prunicola (Murr.) Sacc. & Trott.	116
P. punctata Fr.	101, 105,* 114
P. setigera Peck	110†
P. subiculosa (Peck) Cooke	93
P. superficialis (Schw.) Cooke ex Overh.	105, 108
P. tsugina (Murr.) Sacc. & Trott.	94†
P. unita Fr. non Pers. ex Bres.	109
P. viticola (Schw.) Cooke ex Overh.	105, 108
P. Weirii (Murr.) Sacc. & Trott.	107
P. Xanthospora Undw. ex Lloyd	110
Trametes isabellina Fr.	105, 108
T. odorata (Wulf.) Fr.	96†
T. pini Abietis Karst.	105
T. protracta Fr. ex Shope	96
T. sequoiae Copeland	95
T. setosus Weir ex Overh.	105, 108
T. tenuis Karst. ex Shope	105, 108

SOME LITTLE KNOWN AND UNKNOWN BROWN PLANTS WHICH HAVE NOT BEEN COLLECTED IN THE REGION OF THE LAKE STATES

Fomes tropicalis Cooke (*Grev.*, 15 : 22. 1886). — *Fomitiporia tropicalis* Murr. This plant, reported (14) from Nicaragua, Jamaica, and Guiana, has not been found in the states bordering the Great Lakes.

Polyporus palmicola Berk. & Curt. (*Journ. Linn. Soc. Bot.*, 10 : 317. 1868). — This plant is a tropical one. The type was found in Cuba.

Poria albobrunnea Petch ("Ceylon Polypori," *Ann. Royal Bot. Gard. Peradeniya*, 6 : 51. 1916). — The cotype at Kew is now "tawny-olive." Pore mouths averaging 4–5 to a mm.; tubes 1–2 mm. long, but mostly 1 mm.

Poria altocedronensis (Murr.) Sacc. & Trott. — *Fomitiporella altocedronensis* Murr. (*North Am. Flora*, 9 : 12. 1907). *P. altocedronensis* is known only from the type locality in Cuba (14).

Poria apposita Lév. (*Champ. Mus.*, p. 141, ex. Sacc., *Syll. Fung.*, 6 : 326. 1888).

Poria bicolor Bres. (*Ann. Mycol.*, 18 : 37. 1920). — Tropical. "Obs. Poriae contiguae Pers. affinis, sed optime distincta" (4). *Poria bicolor* E. et Long = *Poria nigrescens* Bres. in Sacc., *Syll. Fung.*, 23 : 431. 1925.

Poria byssogena Jungh. (*Crypt. Jav.*, p. 43, ex Sacc., *Syll. Fung.*, 6 : 329. 1888).

Poria carteri Berk. (*Grev.*, 15 : 25. 1886). — Tropical. "Pores much smaller than any other ferruginous species."

Poria cinchonensis (Murr.) Sacc. & Trott. — *Fomitiporia cinchonensis* Murr. (*North Am. Flora*, 9 : 10. 1907). *P. cinchonensis* has not been found in the region of the Great Lakes. It is known only from Cinchona, Jamaica (14).

Poria cinereo-umbrina P. Henn. (Voeltzkow, *Reise, Ostafrika*, 3 : 19. 1908. Tab. II, Fig. 8, ex Sacc., *Syll. Fung.*, 21 : 327. 1912). — This plant is probably allied to *P. ferruginosa.*

Poria coruscans (Murr.) Sacc. & Trott. — *Fuscoporella coruscans* Murr. (*North Am. Flora*, 9 : 7. 1907). — This plant was described from material collected at Alto Cedro, Cuba. It has not been found in the region of the Great Lakes.

Poria costaricensis (Murr.) Sacc. & Trott. — *Fuscoporella costaricensis* Murr. (*North Am. Flora*, 9 : 7. 1907). This plant is not known in this region. *P. costaricensis* has been reported in Costa Rica.

Poria cribosa. — Lloyd (8) states: "This was based on one specimen from Helvetia still in Persoon's herbarium. It belongs to the ferruginous section with abundant colored setae and small superficial pores. I doubt if it is well developed."

Poria crustosa Speg. (*Fung. Fueg.*, n. 71, p. 32, ex Sacc., *Syll. Fung.*, 6 : 328. 1888). — The affinities of this plant are probably with *P. ferruginosa.* Not known under this name.

Poria cryptacantha Mont. (*Cent.*, 7 : 37, ex Sacc., *Syll. Fung.*, 6 : 329. 1888). — This ferruginous plant has not been found in the region of the Great Lakes.

Poria cubensis (Murr.) Sacc. & Trott. — *Fomitiporia cubensis* Murr. (*North Am. Flora*, 9 : 8. 1907). This brown poria has

been collected in Cuba and Costa Rica (14). Not known from the region of the Great Lakes.

Poria (or Fomes) cylindrispora Lloyd. — Lloyd (10) states: "Perennial, resupinate 0.5 -1 inch thick. Context ferruginous (about snuff brown Ridgway). Pores minute, with silvery glancing mouths. Spores hyaline, cylindrical, 2.5–3 × 6–7, smooth. Mr. Weir finds this abundant on *Quercus garryana*. To the eye it is the same as the common *P. punctata* (*Poria obliqua* of American traditions, not Europe), but no other known similar species has cylindrical spores."

Poria Demetrionis (Murr.) Sacc. & Trott. — *Fomitiporella Demetrionis* Murr. (*North Am. Flora*, 9 : 12. 1907). Type specimen from Missouri. Pore mouths 6 7, mostly 6 to a mm.; tubes 2 mm. long, "snuff brown" (Ridg.). This plant is imperfectly understood and is not known from the region of the Great Lakes.

Poria dryophila (Murr.) Sacc. & Trott. — *Fomitiporella dryophila* Murr. (*North Am. Flora*, 9 : 8. 1907). The type was found in Mississippi on a decayed live oak stump. It is reported from Georgia, Florida, and Mississippi (14). Not known.

Poria Earleae (Murr.) Sacc. & Trott. — *Fomitiporia Earleae* (*North Am. Flora*, 9 : 9. 1907). *P. Earleae* is allied to *P. punctata*. Pore mouths 4–5 to a mm.; tubes up to 2 mm. long, "buckthorn brown" (Ridg.). The type was collected on dead oak branches at Biloxi, Mississippi.

Poria fatavensis Reichardt (*Fungi Hep. et Musci*, p. 141, ex Sacc., *Syll. Fung.*, 6 : 321. 1888).

Poria ferrugineo-velutina P. Henn. (*Fungi Amaz. IV, Hedw.*, 44 : 59. 1905. — *Poria ferrugineo-velutina* P. Henn. = *Pol. lionoides M. resupinatus* in Sacc., *Syll. Fung.*, 23 : 432. 1925.

Poria flavomarginata (Murr.) Sacc. & Trott. — *Fomitiporia flavomarginata* Murr. (*North Am. Flora*, 9 : 11. 1907). The type specimen was collected at Alto Cedro, Cuba. It appears that this plant is closely allied to, if not identical with, *P. punctata*.

Poria floccosa Fr. (*Hym. Eur.*, 572. 1874). Uppsala. Pore

mouths rather large, 2 to a mm.; tubes up to 4 mm. long. The plant so labeled at Uppsala is allied to, and probably conspecific with, *Trametes isabellina* Fr. (*Polyporus tenuis* (Karst.) Romell).

Poria floridana (Murr.) Sacc. & Trott. — *Fomitiporella floridana* Murr. (*North Am. Flora*, 9 : 14. 1907). This plant is known, according to Murrill (14), only from the type locality in Florida.

Poria fuligo (Berk. & Br.) Cooke (*Journ. Linn. Soc.*, 14 : 53. 1875). — This is a charcoal-black plant. A specimen from Ceylon is to be found at Uppsala, Sweden. The plant ex Herb. Berk. at Kew is very thin (about 1 mm. or less). Not known from the region of the Great Lakes.

Poria fusco-lutescens Fr. (*Hym. Eur.*, 570. 1874). — Uppsala.

Poria jamaicensis (Murr.) Sacc. & Trott. — *Fuscoporia jamaicensis* Murr. (*North Am. Flora*, 9 : 11. 1907). *P. jamaicensis* is known only from the type locality (14).

Poria juniperina (Murr.) Sacc. & Trott. — *Fuscoporia juniperina* Murr. (*North Am. Flora*, 9 : 4. 1907). This plant has not been found in this region. The type was collected at St. Martinsville, Louisiana.

Poria labyrinthica Karst. (*Hedw.*, 30 : 298. 1891). — Probably related to, or conspecific with, *P. ferrugineo-fusca* Karst. *vetusta*. See Sacc., *Syll. Fung.*, 23 : 432. 1925.

Poria Langloisiana (Murr.) Sacc. & Trott. — *Fomitiporella Langloisiana* Murr. (*North Am. Flora*, 9 : 13. 1907). "Margin thin, adnate, ferruginous-fulvous, not blackening with age" (14). Type collected near St. Martinsville, Louisiana.

Poria Langloisii (Murr.) Sacc. & Trott. — *Fomitiporia Langloisii* Murr. (*North Am. Flora*, 9 : 9. 1907). Tubes as long as 4.5 mm.; pore mouths 5–7 to a mm., slightly "wood brown"; margin "tawny-olive" (Ridg.). The name *P. Langloisii* was given to a plant collected near St. Martinsville, Louisiana. This poria is allied to *P. punctata* and may be conspecific with it.

Poria Lloydii (Murr.) Sacc. & Trott. — *Fomitiporia Lloydii* Murr. (*North Am. Flora*, 9 : 10. 1907). Not known. Closely

allied to *P. punctata*. Pore mouths 6–7 to a mm., "Prout's brown" to "bister" (Ridg.); tubes as long as 4 mm. The type was collected in Ohio on dead sassafras.

Poria Loennbohmii Karst. (*Fungi nov. Loennb.*, 1904, p. 8 [Finska Vetensk. Soc.] ex Sacc., *Syll. Fung.*, 17 : 135. 1905).

Poria luctuosa Cesata (*Myc. Born.*, p. 7, ex Sacc., *Syll. Fung.*, 6 : 307. 1888).

Poria ludoviciana (Murr.) Sacc. & Trott. — *Fuscoporella ludoviciana* Murr. (*North Am. Flora*, 9 : 6. 1907). — The type of this brown plant was collected on oak at St. Martinsville, Louisiana. *P. ludoviciana* is not known in this region.

Poria Maxoni (Murr.) Sacc. & Trott. — *Fomitiporia maxoni* Murr. (*North Am. Flora*, 9 : 11. 1907). The type was collected on a hardwood log in Costa Rica. It is known only from the type locality (14).

Poria megaloporia (Pers.) Fr. (*Hym. Eur.*, 581. 1874). A specimen of this poria was sent to me by H. Bourdot, "No. 14882 des récoltes de M. Galzin." The wide sterile margin in young portions of the collection and the tubes are mostly "buffy brown" (Ridg.). The tubes are long, mostly 6 mm. Bourdot and Galzin (3) give the spore measurements as 4.5–5–7 × 3.5–4 μ. This plant is very distinct from any of the plants which have thus far been found in the region of the Great Lakes.

Poria mexicana (Murr.) Sacc. & Trott. — *Fuscoporella mexicana* Murr. (*North Am. Flora*, 9 : 7. 1907). Murrill (14) states that it is known only from the type locality in Mexico.

Poria nebulosa Berk. et Curt. (*Journ. Linn. Soc.*, 10 : 317. 1868). — Tropical.

Poria nicaraguensis (Murr.) Sacc. & Trott. — *Fuscoporia nicaraguensis* Murr. (*North Am. Flora*, 9 : 6. 1907). *P. nicaraguensis* has not been found in this region.

Poria obliqua (Pers.) Quél. (Fries, *Hym. Eur.*, 570. 1874). — Uppsala. The European interpretation of this species is different from that of the early American workers. *Poria punctata* has been called *P. obliqua* in America (10). The plant labeled *Pol. obliquus* Per. Fr. at Uppsala appears to me to be *Pol. glomeratus*. Bourdot and Galzin (3) state: "pores

. . . jaune olivace puis brun . . . spores subhyaline, puis fulvescentes, largement elliptique ou subglobulenses, 5–10 × 4.5–7.5 μ, jaune sulfurin en masse." These spore measurements more nearly correspond to those of Bresadola. He gives 9–11 × 6–8 μ for the spore measurements. These measurements do not correspond to those given by Rea (19). Rea states for *P. obliqua* (Pers.) Quél.: "spores white, globose, 4–5 μ."

Poria perparadoxa Speg. (*Fung. Arg. Pug.*, 4, No. 25, ex Sacc., *Syll. Fung.*, 6 : 326. 1888). — South American.

Poria phytoderma Speg. (*Fung. Guar. Pug.*, 1, No. 51, ex Sacc., *Syll. Fung.*, 6 : 308. 1888). — South American.

Poria Ravenalae B. and Br. (*Journ. Linn. Soc.*, 14 : 53. 1875). — This black species is tropical. It is closely allied to *P. fuligo*.

Poria resupinata (Bolt.) W. G. Sm. = *Fomes resupinatus* (Bolt.) Massee, as recorded under *P. obliqua* (Pers.) Quél., by Rea (19). The spore measurements given by Rea for *P. obliqua* are "globose, 4–5 μ," whereas under *F. resupinatus* the spores as recorded by Massee are given as "elliptical, 4 × 1.5 μ."

Poria Rickii Bres. (*Ann. Mycol.*, 18 : 37. 1920). — "A *Poria umbrinella* Bres., cui simillima, differt mycelio sulphureo, sporis vix coloratis, hyphis contextus majoribus et praesentia setulorum in hymenio" (4).

Poria rufitincta Berk. & Curt. (Herb. Kew, *Grev.*, 15 : 25. 1886). — "Ad truncos, Cuba. Never described. Does not appear to differ from *P. ferruginosus* except in the minute, regular, round pores."

Poria separabilis Karst. (*Symb. Myc. Fenn.*, 25 : 21, ex Sacc., *Syll. Fung.*, 9 : 193. 1891).

Poria setulosa P. Henn. (*Engl. Jahrb.*, 28 : 321. 1900, ex. Sacc., *Syll. Fung.*, 16 : 161. 1911). — In speaking of a collection received from a collaborator, Lloyd (13) states: "The plant was named from Africa, but is principally known from the Philippines." Lloyd believed it to be allied to *Polystictus cervino-gilvus*.

Poria Shaferi (Murr.) Sacc. & Trott. — *Fuscoporella Shaferi*

Murr. (*North Am. Flora*, 9 : 7. 1907). Murrill (14) states that it is known only from the West Indies.

Poria sorbicola Fr. (*Hym. Eur.*, 570. 1874). — Uppsala. This ferruginous plant is not known in the region of the Great Lakes.

Poria subobliqua P. Henn. (*Engl. Jahrb.*, 38 : 108. 1905. Ex Sacc., *Syll. Fung.*, 21 : 328. 1912).

Poria tenerrima B. et Rav. (*North Am. Fungi*, n. 153, Rav. *Fung. Car. Fosc.*, 3, n. 13, ex Sacc., *Syll. Fung.*, 6 : 333. 1888). — *Ulmus americana.* This is a very thin plant; the tubes are less than 0.3 mm. long. Pore mouths 3 to a mm., about "Prout's brown" (Ridg.).

Poria umbrina Fr. (Fr., *Hym. Eur.*, 571. 1874). — Uppsala. Listed by Rea (19) "as *Polyporus ferruginosus* Fr." *Pol. umbrinus* Pers. = *Fomes obliquus* Fr. in Sacc., *Syll. Fung.*, 6 : 206. 1888.

Poria umbrinella Bres. (*Hedw.*, 35 : 282. 1896). — *Fomitiporella umbrinella* (Bres.) Murr. This plant is chocolate-colored. The type was collected in the state of Santa Catharina, Brazil. It has not been found in Michigan.

Poria undulata (Murr.) Sacc. & Trott. — *Fomitiporia undulata* Murr. (*North Am. Flora*, 9 : 10. 1907). Murrill (14) reports that this is known only from the type locality — near Punta Gorda, British Honduras.

Poria unita Pers. (*Hym. Eur.*, p. 570. 1874). — Uppsala. See No. 109, *P. ferrugineo-fusca* Karst., in key. *P. unita* Pers. non Fr. = *Poria megaloporia* Pers. in Sacc., *Syll. Fung.*, 23 : 432. 1925.

Pol. vinosus Berk. = *Pol. badius* Jungh. in Sacc., *Syll. fung.*, 23 : 1–1026. 1925. The color of *Pol. vinosus* is close to that of *P. niger*, according to Bresadola.

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PLATES XLI-L

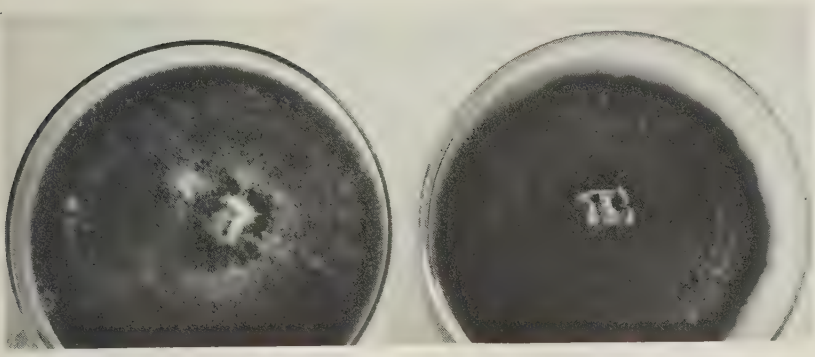


FIG. 1. *Fomes nigricans* (*F. igniarius* var. *nigricans*) from *Betula alba*, cultured in the light and in the dark

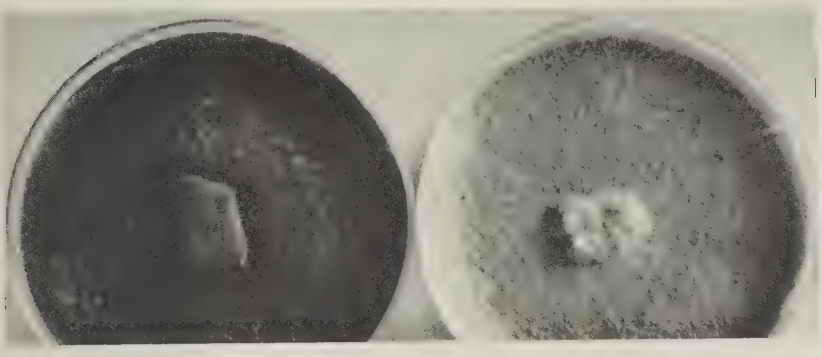


FIG. 2. *Poria betulina* from *Betula alba*, cultured in the light and in the dark

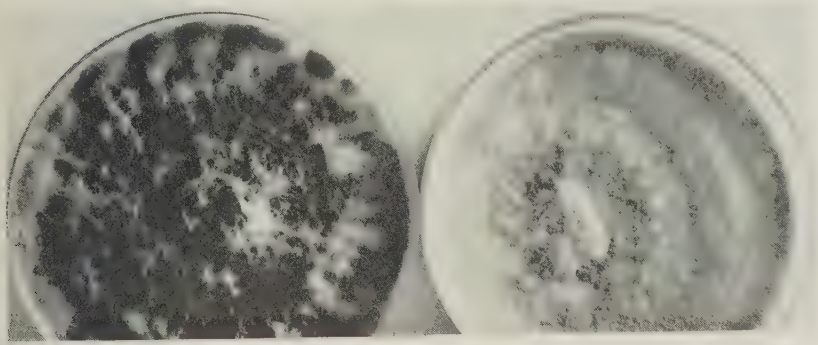


FIG. 3. *Poria prunicola* from *Prunus serotina*, cultured in the light and in the dark

PLATE XLII

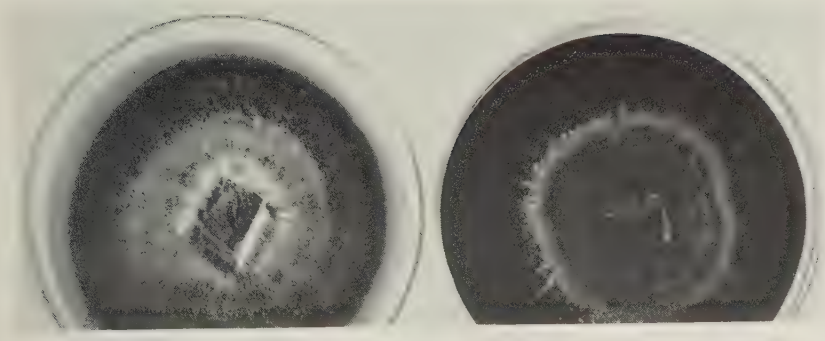


FIG. 1. *Fomes nigricans* (*F. igniarius* var. *nigricans*), cultured on malt and Czapek agar

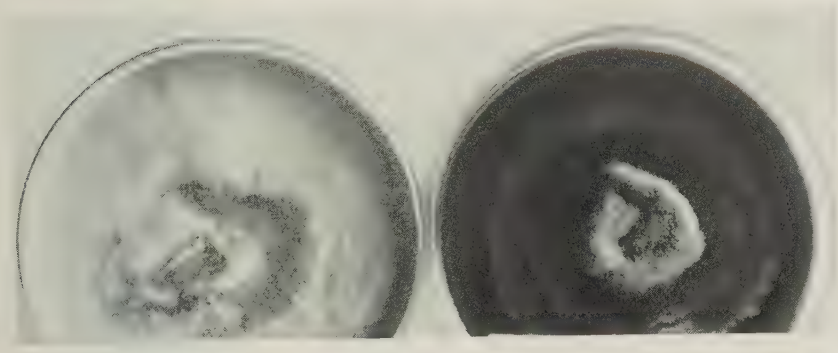


FIG. 2. *Poria betulina*, cultured on malt and Czapek agar

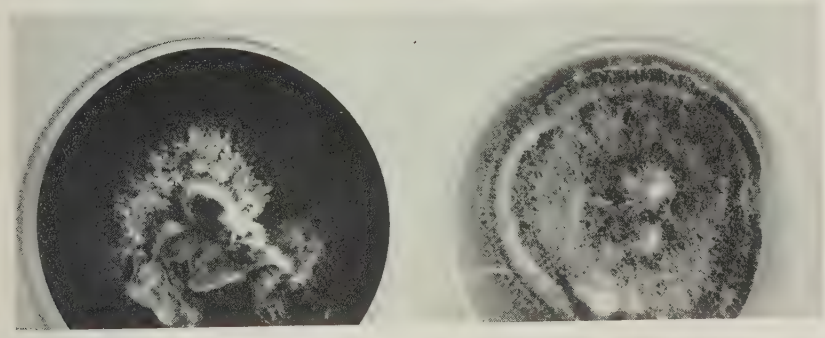
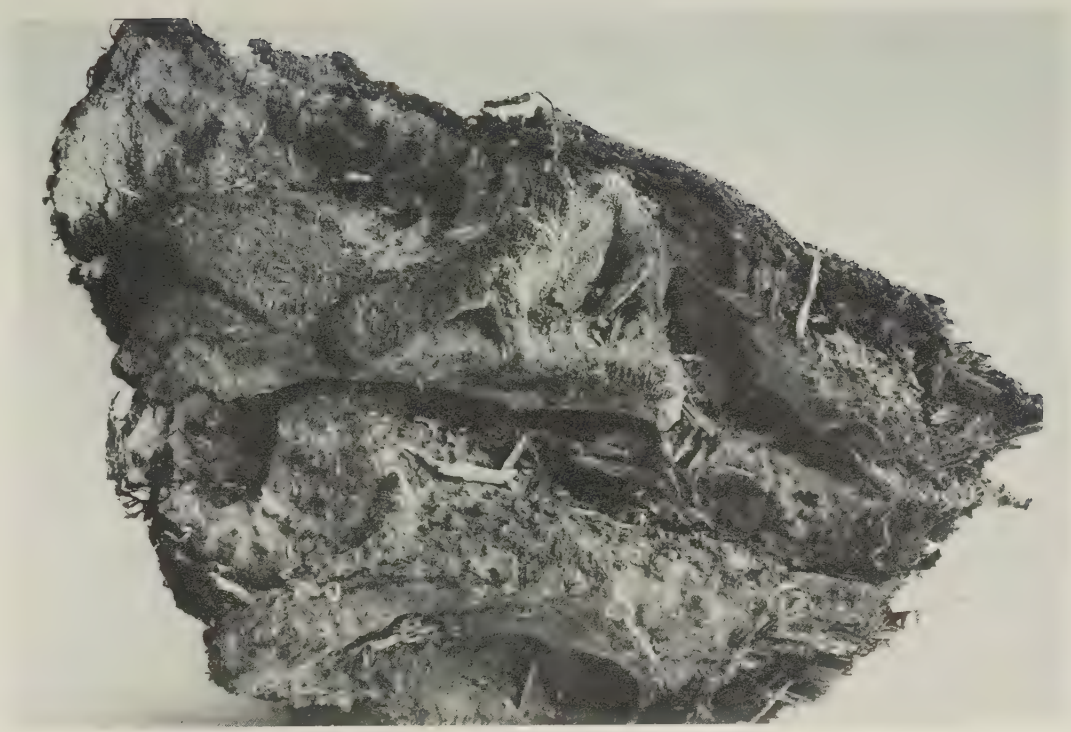


FIG. 3. *Poria prunicola*, cultured on malt and Czapek agar

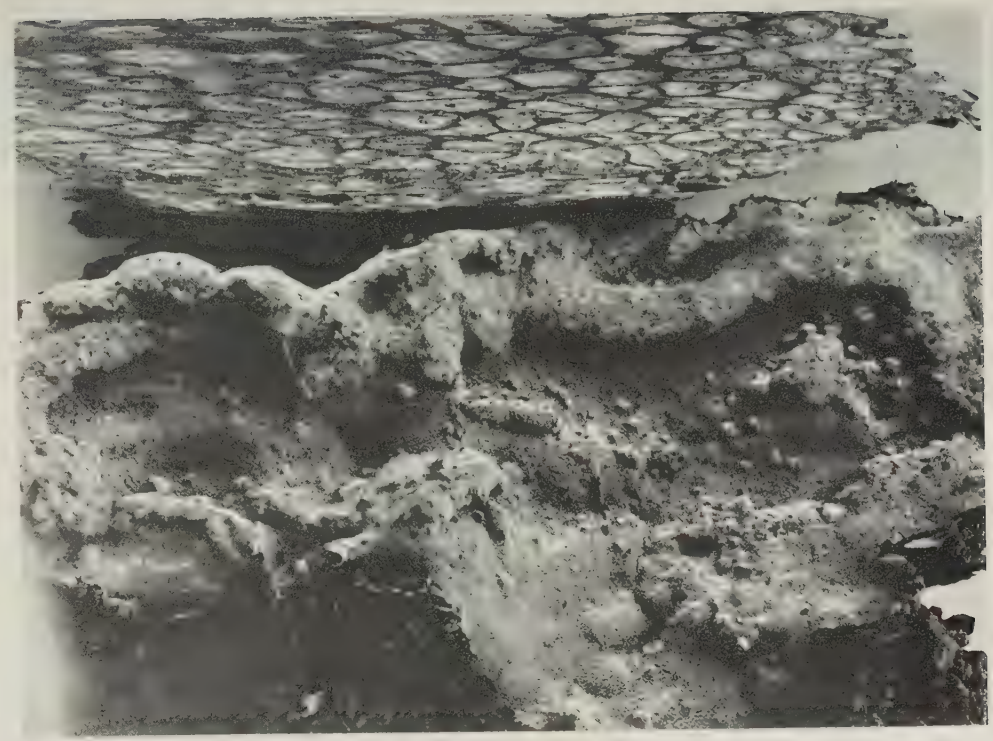
PLATE XLIII



Poria subiculosa (Peck) Cooke. Isle Royale, Michigan

PLATE XLIV

Fomes robustus Karst. on upper part of oak tree, Stockholm, Sweden



Fomes nigrolimitatus Romell on *Tsuga mertensiana*, Crater Lake, Oregon

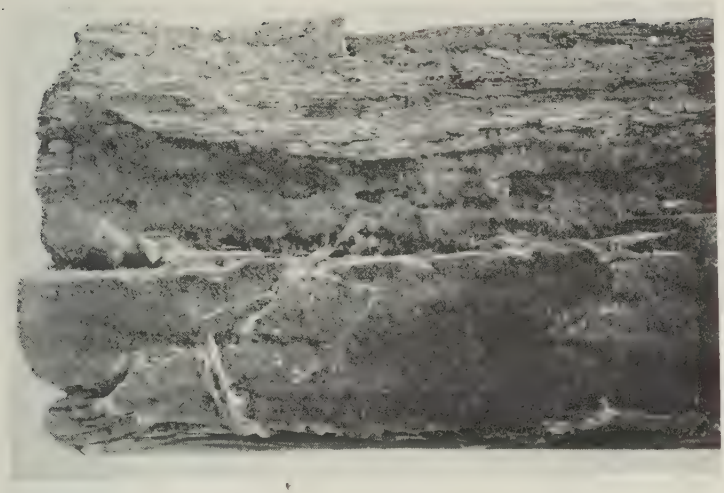


FIG. 1. *Poria ferruginosa* Fr. on *Thuja occidentalis*, Atlanta, Michigan

FIG. 2. *Polyporus glomeratus* Peck on *Ulmus americana*, Lakeland, Michigan

PLATE XLVII

Polyporus glomeratus Peck on yellow birch, Superior National Forest, Minnesota

FIG. 1. Rot in Crataegus wood caused by *Fomes pomaceus* Pers. forma *Crataegi*. Ann Arbor, Michigan

FIG. 2. Longitudinal section of Crataegus wood. Rot caused by *Fomes pomaceus* Pers. forma *Crataegi*. Ann Arbor, Michigan

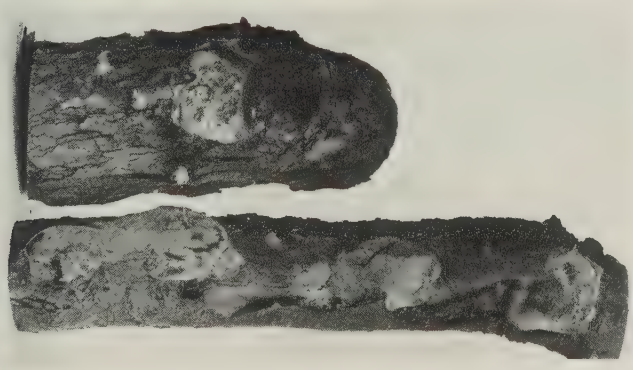


FIG. 3. *Fomes pomaceus* Pers. forma *Crataegi* on *Crataegus sp.* Ann Arbor, Michigan

PLATE XLIX

FIG. 1. *Poria prunicola* (Murr.) Sacc. & Trott. (young plant) on *Prunus serotina*, Ann Arbor, Michigan

FIG. 2. *Poria prunicola* Sacc. & Trott. on *Prunus serotina*, Grand Island, Michigan

PLATE L

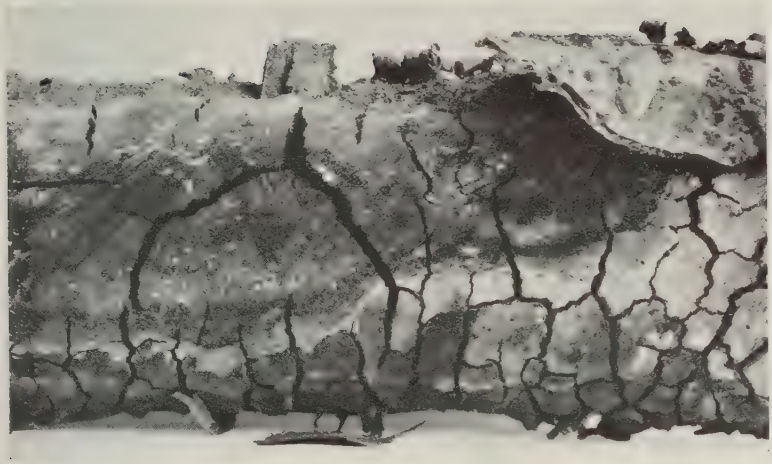


FIG. 1. *Poria prunicola* on *Prunus serotina* (old plant), Sugar Island, Michigan

FIG. 2. *Fomes igniarius* var. *laevigatus* on birch log, Superior National Forest, Minnesota

AN INVENTORY OF MICHIGAN STATE FOREST PLANTATIONS

GEORGE S. McINTIRE

FOR more than twenty-five years the State of Michigan has carried on a more or less extensive planting program. The beginning was necessarily small, and the average annual planting prior to 1910 consisted of only one or two forty-acre tracts. The state forests, however, have gradually but steadily increased in area and number, a field organization has been built up, and a nursery with an annual production capacity of 20,000,000 trees has been developed. Reforestation has kept pace with these other operations, and in 1931 the peak was reached with a planting of more than 30,000 acres, bringing the total area reforested up to 129,000 acres. Previous to 1910 only 242 acres had been planted. This area increased gradually till 1927, when the annual planting was about 7,500 acres. Since that time progress has been even more marked, and the plantings of the last four years total more than three fourths of the entire reforested area.

Since the first state forest was organized in 1903 methods involving a score of species have been employed, and more than seventy combinations of stock ranging from direct seeding to the use of four- and five-year transplants have been tried out. It soon became evident that comparatively few species were able to endure the conditions which were typical of the state forest areas. As time went on, it became more and more apparent that there was little hope of obtaining favorable results by the use of any species except native ones possessed of characteristics which had been developed on these potential planting areas, namely, jack, Norway, and white pine.

There are a number of factors which prohibit the planting of

more exacting species. We now have twelve state forests totaling 1,400,000 acres, slightly over half of which is state land. Ownership has been acquired largely through the tax-delinquent route, and in general is confined to lands of inferior quality known as the pine plains and the oak and pine hills. This condition is aptly illustrated by a planimeter study which was made of the soil conditions on 700,000 acres of state forest lands for which soil maps were available. The results of this study were significant in that 78 per cent of this entire area and 92 per cent of the uplands were made up of the light, sandy soils on which forests of pine were the principal virgin growth.[1] These figures apply regardless of ownership. It is worthy of note, however, that state ownership runs comparatively low on the better soils represented by the 8 per cent of the upland area. Furthermore, if fire is kept out, cut-over hardwood lands adequately restock without planting. For example, Land Economic Survey maps of Alpena, Roscommon, Ogemaw, Crawford, and Kalkaska counties show a hardwood area of 100,000 acres, of which only about one fourth is poorly stocked. This figure included recently cut slash areas on which reproduction had not yet become established, together with a considerable area of heavily grazed lands near farm communities in which typical state forest conditions do not exist. Because of these various factors prospective planting sites of a quality to insure the growth of more exacting species than the native pines are of comparatively small area, and on most state forests their extent is practically negligible.

One of the most pertinent factors in any extensive planting program is the cost. This is determined not only by the character of the soil and the natural growth, but also, to a large degree, by the accessibility and size of the tracts to be planted. Other things being equal, large blocks are planted most cheaply, and as the areas become patchy, small, and more isolated from the other tracts, the cost of planting soon becomes prohibitive.

[1] Exceptions to this are the Mackinac, the Hardwood, and the Pigeon River tracts, all of which contain large areas of hardwood lands, but which, except a part of the Pigeon River tract, are comparatively young as state projects.

Large units of prospective planting areas are essential to any extensive planting program, and the pine lands represent the only set of conditions within the state forest boundaries which would admit a planting operation of any considerable magnitude. The less exacting native pines are the only answer for such a program.

It is true that these areas are of inferior site quality. They were so, under virgin conditions, and repeated burns have further reduced their capacity. But pines are volume producers, and we may slide far down the scale of Norway pine site classes and produce a better and faster volume than can be attained on hardwood sites of greater natural fertility by the more exacting hardwood species. Even on Grayling sand, which is the poorest as well as perhaps the most extensive of the more generally distributed sandy plain soils, Norway and not jack pine was once the principal growth. Rubicon sand, also a plain soil, is of slightly better site quality; whereas Roselawn sand, of morainic origin, ranks slightly above Rubicon sand. These three soil types constitute the bulk of the denuded and poorly stocked state forest areas. They are of inferior site quality, but they once supported excellent stands of pine.

The forty-acre tract has always been considered the planting unit on the state forests. Complete records of each planted forty or portion of a forty, consisting of the following material, are on file:

1. A large-scale map indicating:
   (*a*) The nature of the ground cover,
   (*b*) The volunteer forest growth,
   (*c*) The location of the planting;

2. A planting report stating:
   (*a*) The year and season of planting,
   (*b*) The species and class of stock,
   (*c*) The spacing and number of trees per acre,
   (*d*) The method of preparation and planting.

To supplement further these records with information as to their progress a study was made of the older plantations during the summer of 1931. In order to cover an area of sufficient size to portray a cross-section of the various conditions this survey

was primarily extensive in character. A two-man crew was employed, and the field work consumed approximately one hundred man days. Only plantations five or more years old were considered, for the following reasons: (1) it was felt that growth rate based on younger trees would not necessarily be an index of what might be expected later; (2) survival figures for plantations on dry, sandy soils mean little for plantings less than five years old.

The area studied was distributed over the Fife Lake, Alpena, Ogemaw, Higgins Lake, and Presque Isle state forests, and represented 45 per cent of all plantations of sufficient age to be examined. The amount of strip line was totaled as 14,234 chains, and, with acreage deducted for roads and fire lines, an actual net planted area of 14,473 acres was covered. Two other forests, the Pigeon River and the Houghton Lake, contained plantations of adequate age and extent to qualify for the study. It was originally intended to include both these units, but sufficient time and money were not available.

Owing to the extensive nature of the survey and the comparatively young age of most of the plantations, only information on average height and number of trees was recorded. In order to correlate the reaction of the planted species with various natural conditions the soil type was determined, a record was made of the ground cover, and a complete tabulation was made of the species, size, and distribution of the volunteer forest growth.

All changes in height, density, and composition of either the planted stock or the volunteer forest growth, together with marked variations in the character of the ground cover or soil conditions, were indicated on a large-scale plat, which also carried the location of the strip line.

In general, two strips five chains in from the side were run across each forty-acre tract, giving approximately forty chains of strip to each description. At times the locations of the strips were shifted to obtain a better representation of all parts of the area, and, upon a few occasions, when conditions seemed uniform over the entire forty, only one strip was run, usually through the center.

The data were recorded on three forms. Two were preliminary, and the third sheet carried a summary of the others, together with the plat on which the mapping was done. A count of the planted stock in one row was made, and the number of trees for each chain of strip was tallied on the first form, by species. The average height to the nearest quarter foot for each species, together with the names of the two predominating species of ground cover, was tabulated directly opposite the figures representing the number of trees for that particular chain of strip. In addition, a space was reserved below for a fuller description of the ground cover. On the second form the volunteer forest growth was tallied on a strip 6.6 feet wide, by the Lowdermilk mil-acre method. By this process the mil-acres or 6.6-foot squares in each chain of strip which were stocked with one or more trees, were recorded in the column for that particular species. In this way distribution in particular was stressed. No attempt was made to count the actual number of volunteer trees on the strip, and the inconsistency of a patchy stocking which could not be taken care of in a mere count was eliminated. From the data recorded on these two forms the condition of the soil, ground cover, volunteer growth, and planted stock may be ascertained and worked up with regard to the segregation of areas on the basis of changes in any of these conditions.

The stocking per acre of the volunteer growth was determined on a mil-acre basis direct from the preliminary forms. A somewhat different process was employed in working up per acre figures for the planted stock. In the first place, it was not necessary to guard against irregular and patchy stocking on areas too small to be segregated, as in the case of the volunteer growth. In the second place, an interval 6.6′ by 6.6′ was not employed in the planting operations. The spacing of the rows on each plantation was taken from the original planting records, and by means of this figure the number of chains of rows per acre was obtained. This result, when multiplied by the average number of trees per chain of strip, gives the average number of trees per acre for that particular area.

A two-chain tape without a trailer was used and was secured

at each end by a twelve-inch steel pin. Each tenth link was painted red to designate the mil-acre limits. A head and a rear chainman made up the field party. The head chainman mapped the area and recorded the ground cover and the planted stock; the rear chainman snubbed the chain and recorded the volunteer growth. Both men were able to make their counts as they went forward. In this way all back-tracking was eliminated. Each man entered his tabulations as the other was making his count. This system was employed after several had been tried out and proved to be just as exact as any of the others and 30 per cent less time-consuming.

On some plantations, particularly those which had not been furrowed and on which occurred patchy clumps of the same species as those which had been planted, it was impossible to separate the planted stock from the volunteer growth. Such plantations were of necessity excluded from the study. This was the only limiting factor in deciding which descriptions should be included. Otherwise, the plantations were worked as we came to them, and the poor were included along with the good.

The 14,473 acres worked were distributed among the various types of plantings as follows:

	Acres
Mixed plantations of Norway and jack pine	7,159
Pure jack pine plantations	2,780
White pine underplantings	2,616
Miscellaneous plantings consisting mostly of open plantings of either white or Scotch pine mixed with some other species	1,918

The figures for all species of all ages for the entire area worked were:

Total average age of the plantations	9 years
Total average height	6 feet
Total average number of trees per acre	529

The height and age figures were multiplied by the number of acres in each plantation or part of the plantation to which they applied. These results when added together and divided by the total number of acres gave the figures indicated above for total average age and total average height. The total average number of trees per acre was computed on a like basis.

These results are very general, but they become more significant when supplemented by graphs. Figure 42 indicates the proportion occupied by each of the various soil types in the area studied. It is worthy of note that only 72 acres (Griffin sandy loam and Selkirk silt loam) originally grew upland hardwood species;

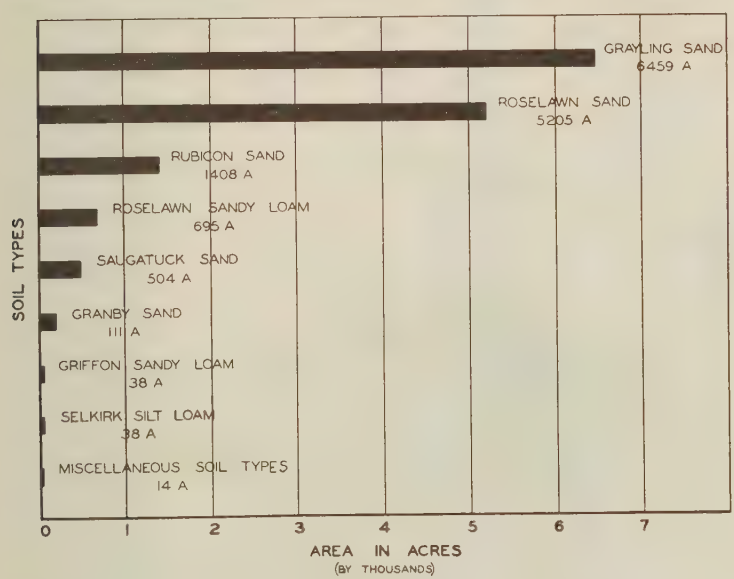


Fig. 42. Area occupied by each soil type

111 acres (Granby sand) was made up of semiswamp lands on which the virgin forest consisted of a mixture of swamp hardwoods and swamp conifers. The remaining 14,290 acres supported a virgin growth which was mainly pine.

Figure 43 signifies the area included in each 100-tree-per-acre stocking class. The small area of heavily stocked plantations ranging from 1,100 to 1,700 trees per acre is accounted for by the very early plantings on which the trees were spaced much closer than those planted more recently.

Figure 44 shows the average number of jack and Norway pine

per acre for each one-year age class on those plantations on which the two species were planted in mixture. In every age class

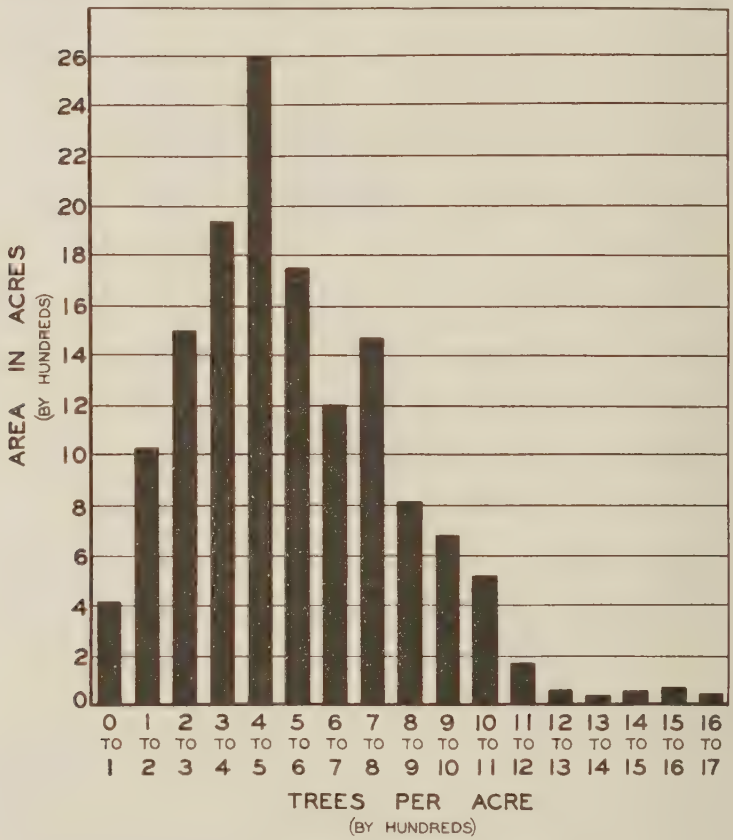


Fig. 43. Area in each one-hundred-tree-per-acre stocking class

the number of jack pine exceeds that of Norway. In most plantations, however, the number of Norway is sufficient to produce eventually a good stand and in a few places is more abundant than the jack pine. On the other hand, there are plantings where

the jack has developed favorably and the Norway has failed completely. Such results are often impossible to forecast, which is one of the reasons for planting in mixture.

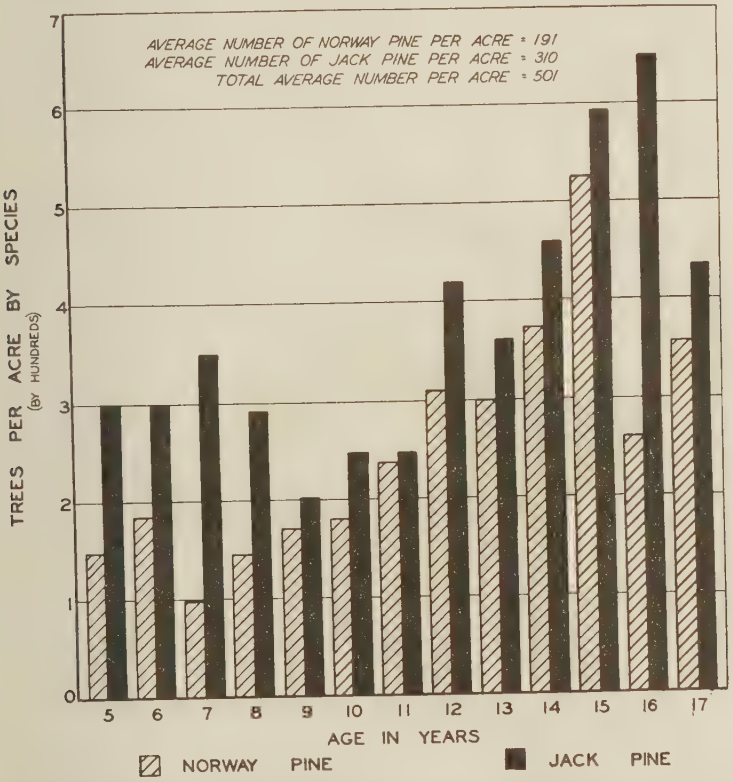


Fig. 44. Average number of jack and Norway pine per acre in mixed plantings

Figure 45 is a comparison of height growth made by Norway and jack pine planted in the open and white pine in the underplantings. Although the growth rate of white pine under these conditions has been slow, the survival has in general been very satisfactory. The curve for jack pine indicates an increased

growth over Norway at the start, but despite the low age for which figures were available the latter species is already showing a marked tendency toward early dominance.

In considering these figures and graphs several factors should

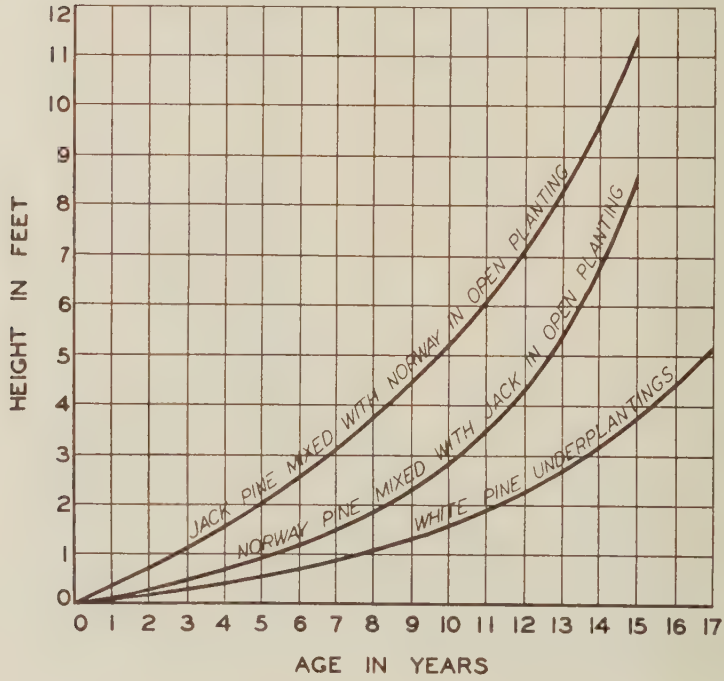

HEIGHT IN FEET
AGE IN YEARS
JACK PINE MIXED WITH NORWAY IN OPEN PLANTING
NORWAY PINE MIXED WITH JACK IN OPEN PLANTING
WHITE PINE UNDERPLANTINGS

Fig. 45. Height growth by one-year age classes

be kept in mind. Many of the earlier planting methods on which these results were based are no longer in practice. A number of species, Scotch pine, for example, are not now used. The more selective "interplanting" method, requiring fewer trees and with mixed stands as an objective, is now practiced instead of underplanting. The latter process has exerted considerable influence in holding down the figure for "total average height," since 2,600

of the 14,000 acres studied were planted by this method. However, planting of this type is comparatively small with relation to the total area planted. Another factor which will bear further emphasis is that, although the plantations range in age from five to twenty-six years, by far the greater acreage falls in the younger age classes, a condition which strongly tends to lower the figure for "total average age." An annual height growth of two feet for all three species is not uncommon on the older plantations.

Although an operation such as this gives a fairly adequate picture of conditions as they exist on the ground, it is primarily of an extensive nature. To obtain full benefit of all the material gathered, it is probable that it should be further supplemented by more intensive studies. To date there has been sufficient time only for the compilation of figures and results of a very general nature. As a matter of fact, I am not over optimistic of our ability to go much beyond this without more intensive field work, since there are so many factors, impossible of isolation, which directly affect tree growth. On the other hand, considerable information has been assembled which could have been obtained only from an extensive reconnaissance.

The areas included in this study represent a potential site capacity which may again be realized with a little careful management. But we must pay the price for the abuse to which these lands have been subjected. Failures have occurred in the past, and we may expect more of them. For a while we must be content to have jack pine in some places where Norway and white once grew. As in all rebuilding jobs, reforestation is a tedious process. But perhaps, after all, we might do well to duplicate some of the practices of countries with longer experience in forestry, where more attention has been given to the building up of site capacity, and less emphasis placed on immediate returns.

Department of Conservation,
Lansing, Michigan

AN ANALYSIS OF CARRYING CHARGES ON MERCHANTABLE TIMBERLANDS IN UPPER MICHIGAN

WILLETT F. RAMSDELL

DURING the past twenty-five years the movement to encourage the practice of forestry, that is, timber cropping instead of timber mining, has been under way and growing throughout the United States. A review of the present situation in the Lake States shows, with a few outstanding exceptions, very little progress in translating this movement into action or actual practice on the privately owned timberlands. Timber owners and operators in the region, however, are now manifesting more interest than ever before in the possibilities of so-called economic selective cutting as contrasted with destructive clear-cutting, but it is difficult for the operator who may become personally convinced of the merits of this procedure for his tract of timber to persuade in turn his board of directors or his banker. The chief obstacles to greater progress in forestry are very clearly economic and financial. Within the past few years the burden of taxation has been put forth as one of the primary reasons for the widespread policy of immediate and complete liquidation. In this study an effort has been made to learn just what the tax burden does mean to typical holders of merchantable timber in northern Michigan.

SOURCE OF DATA

The following analysis deals with sixteen tracts of merchantable timberland representing eleven owners in eight counties and twenty-one political townships in the Upper Peninsula of Michigan. This last figure is of significance in that the amount of taxes levied upon these sixteen properties from year to year was

arrived at by twenty-one assessing officers (township supervisors), each acting independently of the others. One of the tracts is exceptionally large; the others range from 2,400 to 37,246 acres and total 211,650 acres. For a tract to qualify for inclusion in this study it was necessary for the owner to furnish the following data:

1. The location.
2. A reliable cruise of the present stand by species and products.
3. The tax payments by years for a considerable period down to 1930 inclusive. (For three of the tracts they were given to date of sale, and for the sixteen tracts averaged sixteen and one-half years.)
4. If recently sold, the sale price; and otherwise an estimate of the present market value.
5. When available, accurate information as to purchase price. This was given for eleven tracts.

These requirements necessarily limited the choice of tracts for study, but those selected are believed to be quite representative of the remaining merchantable timber of the Upper Peninsula. Many of the fifteen smaller tracts, averaging 14,110 acres each, were selected as representative of larger holdings and were restricted in size only because of the great amount of office work involved in compiling data on the tax and cruise. Thus in reality the 211,650 acres represent a much larger area of comparable timberland. The total timber stand and average stand per acre for this entire area is as shown in Table I.

The estimate given above is presumed to represent average utilization practice, with all the products merchantable and with positive stumpage values.

ANALYSIS OF YEARLY TAX PAYMENTS

Table II shows the actual taxes per acre for each of the sixteen timber tracts for the period of years for which these data were available, together with the average tax for the five-year period, 1926–30, and the average tax for all tracts involved by years

from 1903 to 1930. During this period there have, of course, been very great variations in the purchasing power of the dollar. There is also given in the tabulation, therefore, the annual average

TABLE I

TOTAL AND AVERAGE PER ACRE STAND ON FIFTEEN TIMBER TRACTS IN THE UPPER PENINSULA OF MICHIGAN

Item	*Total*	*Average per acre*
Number of acres	211,650	....
Board feet, handworked sawtimber	558,958 M.	2,641
Board feet, conifer sawtimber	485,902 M.	2,296
Total of sawtimber	1,044,860 M.	4,937 bd. ft.
Hemlock	37.09%	37.09%
Railway ties, pieces	1,694,909	8.01
Cedar poles, pieces	275,656	1.30
Cedar posts, pieces	3,155,876	14.91
Spruce pulpwood, cords	92,694	0.44
Balsam and hemlock, cords	290,260	1.37
Chemical wood, cords	509,020	2.41
Approximate total Board feet equivalent	1,454,410 M.	6,872 bd. ft.

tax per acre in what might be termed "real" rather than "nominal" money value. The index used is based on weighted wholesale prices of all commodities as published by the United States Bureau of Labor Statistics. The year 1926 represents the base year; that is, the value of the dollar in 1926 is rated at 100, and its value for any other year is a percentage of the 100 base. In this connection it should be borne in mind that the relative spread between the nominal money value taxes and the real money value taxes over the entire period will remain the same, no matter what year is chosen for the base.

Chart 1 (Fig. 46), based upon Table II, shows graphically the actual and curved annual tax per acre for the period 1905 30 in nominal money value and in real money value based on the 1926 dollar. It is interesting to note that, whereas the nominal value curve rises to a peak in 1926, the real value curve rises

TABLE II

TAXES PAID PER ACRE PER YEAR ON SIXTEEN TIMBER TRACTS IN THE UPPER PENINSULA OF MICHIGAN

Year	TRACT NUMBER																AVERAGE TAX PER ACRE	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Nominal value	1926 dollar
1903	.03	....	....	....	....	....	...	...	...	...	...	....	...	....	....	....	.03	....
1904	.06	....	....	....	....	....	...	...	...	...	...	....	...	....	....	....	.06	....
1905	.08	.20	....	....	....	....	...	...	...	...	...	....	...	....	....	....	.14	.24
1906	.07	.17	.16	.19	....	....	...	...	...	...	...	....	...	....	....	....	.15	.25
1907	.08	.22	.22	.22	....	....	...	...	...	...	...	....	...	....	....	....	.18	.29
1908	.09	.21	.19	.24	....	....	...	...	...	...	...	....	...	....	....	....	.18	.30
1909	.11	.24	.25	.22	....	....	...	...	...	...	...	....	...	....	....	....	.21	.33
1910	.12	.34	.22	.24	....	....	...	...	...	...	...	....	...	....	....	....	.24	.36
1911	.14	.38	.25	.09	....	....	...	...	...	...	...	....	...	....	....	....	.22	.36
1912	.15	.52	.38	.23	....	....	...	...	...	...	...	....	.23	....	....	....	.30	.45
1913	.16	.53	.47	.24	....	....	...	...	...	...	...	....	.28	....	.41	....	.35	.52
1914	.17	.63	.39	.27	....	....	...	...	...	...	...	....	.30	.85	.39	....	.43	.66
1915	.25	.84	.49	.29	....	....	...	...	...	...	...	....	.35	1.28	.61	....	.62	.92
1916	.26	1.20	.48	.31	....	....	...	...	...	...	...	.35	.41	1.47	.66	....	.65	.78
1917	.27	1.02	.54	.37	....	....	...	...	...	...	...	.40	.40	1.54	.66	....	.71	.60
1918	.40	.92	.62	.39	.80	....	...	...	...	...	...	.54	.39	1.34	.96	....	.74	.57
1919	.41	1.05	.73	.52	.88	.44	...	...	.46	...	...	.74	.47	1.28	1.28	....	.75	.56
1920	.41	1.02	.87	.60	.83	.58	.34	.49	.47	...	...	.83	.57	1.37	1.30	....	.74	.50
1921	.43	1.28	1.23	.60	.88	.81	.33	.51	.63	.66	.77	.92	.68	1.60	1.45	....	.83	.88
1922	.39	1.24	1.18	.62	.80	.79	.35	.53	.55	.61	.74	.99	.65	1.64	1.46	....	.82	.83
1923	.39	1.44	1.21	.67	.78	.87	.35	.54	.56	.64	.62	1.14	.74	1.96	2.09	....	1.05	1.03
1924	.42	1.92	1.18	.91	.90	1.09	.33	.74	.62	.66	.65	1.17	.81	2.07	2.00	....	1.02	1.03
1925	.39	1.68	.86	.92	.88	1.25	.33	.76	.61	.59	.63	1.22	.77	1.72	2.46	....	1.00	.94
1926	.48	1.54	.84	1.01	1.22	1.13	.34	.82	.62	.58	.62	1.16	.77	1.72	2.28	1.06	1.01	1.01
1927	.53	1.92	1.08	1.08	1.32	1.19	.37	.85	.65	.69	.65	1.20	...	1.67	2.07	1.09	1.09	1.15
1928	.49	1.51	.93	.94	1.19	1.14	.38	.87	.60	.66	.67	.93	...	1.48	....	1.27	.94	.97
1929	.46	1.28	1.09	.94	1.08	1.18	.39	.87	.64	.68	.74	.97	...	....	....	1.46	.91	.94
1930	.50	1.62	1.13	.96	.69	1.20	.42	.88	.72	.69	.71	1.03	...	....	....	1.26	.84	.98
5-year Av.*	.49	1.57	1.01	.99	1.10	1.17	.38	.87	.65	.66	.68	1.04	...	....	....	1.23	.96	1.01

* As applied to the last five years. Chart I (Fig. 46) is based upon Tracts 1–16. Tables III–IV are based upon Tracts 1–11. Chart 2 (Fig. 47) is based upon Tracts 1–12 and 16.

steadily throughout the period, though flattening perceptibly after about 1924. The actual peak year was 1927, when the nominal value tax had risen 800 per cent, from \$0.14 to \$1.09

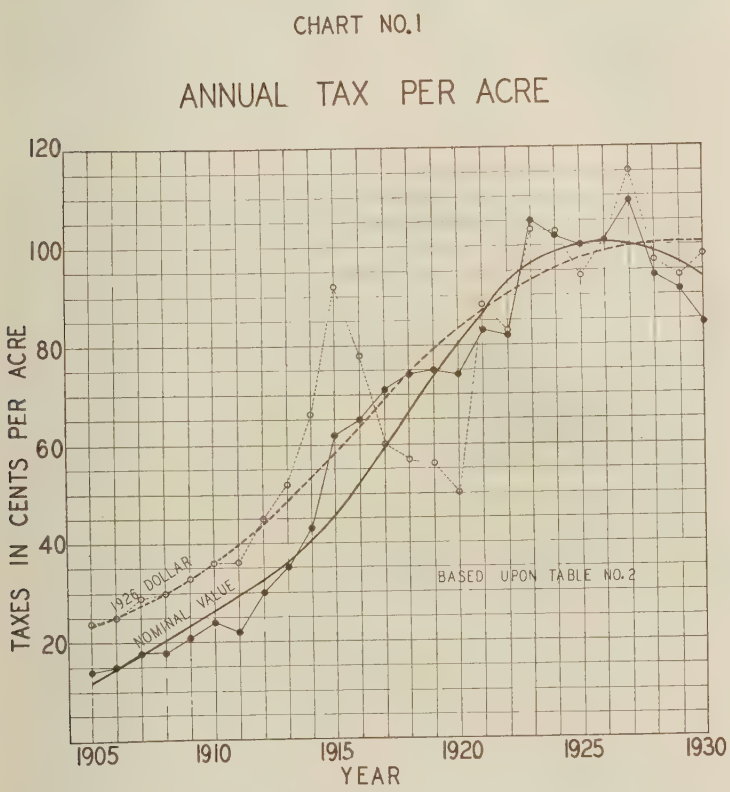


FIGURE 46

per acre, and the real value tax 480 per cent, from \$0.24 to \$1.15. From 1927 to 1930 there is a sharp reduction to \$0.84 and \$0.98, respectively, but with the real money tax figure again on the upward trend, which undoubtedly continued in 1931.

TABLE III

Relationship of Accumulated Costs (6 per cent Compound Interest) to 1930 Inclusive, to the Immediate-Conversion Values of Eleven Merchantable Timber Tracts in the Upper Peninsula of Michigan

Tract no.	Year purchased	Per Acre									
		Six per cent			Six per cent			Total cost	Immediate-conversion value	Difference cost and value	Per cent Tax and Int. of conversion value
		Price	Int.	Total	Taxes	Int.	Total				
1	1903	3.26	16.61	19.87	7.74	5.56	13.30	33.17	13.76	− 19.41	96.6
2	1905	10.00	32.92	42.92	24.92	18.71	43.63	86.55	20.70	− 65.85	211.0
3	1906	11.45	35.00	46.45	16.99	13.01	30.00	76.45	21.79	− 54.66	137.8
4	1906	6.76	19.73	26.49	13.07	10.91	23.98	50.47	22.45	− 28.02	106.9
5	1918	10.81	10.93	21.74	12.25	6.17	18.42	40.16	17.87	− 22.29	103.2
6	1919	41.00	36.90	77.90	11.67	5.83	17.50	95.40	24.48	− 70.92	71.4
7	1920	7.72	6.91	14.63	3.93	1.67	5.60	20.23	13.15	− 7.08	42.6
8	1920	17.50	13.88	31.38	7.86	4.04	11.90	43.28	38.66	− 4.62	30.8
9	1920	33.48	31.12	64.60	7.13	2.97	10.10	74.70	16.71	− 57.99	60.4
10	1921	23.07	15.83	38.90	6.46	2.03	8.49	47.39	17.08	− 30.31	49.7
11	1921	31.85	22.05	53.90	6.13	2.85	8.98	62.88	55.00	− 7.88	16.3
Av. not weighted				39.89			17.45	57.34	23.79	− 33.55	84.2

THE TAX BURDEN RELATED TO THE PROPERTY VALUES INVOLVED

The foregoing data show the steadily mounting tax burden applied to these sixteen tracts of timberland. Obviously, the total burden of carrying charges, as well as the annual charge, varies greatly with each property, dependent for each owner upon:

1. The original purchase price.
2. The number of years owned.
3. The annual tax payments.
4. Other expenditures, such as protection and supervision made for and charged to the timberland.
5. Rates and method of computation of interest on any or all expenditures.

In considering the eleven tracts for which all other data were available it was thought best to eliminate item 4 entirely, and in Table III six per cent compound interest has been applied to purchase price and tax payments. The cases can readily be refigured upon any other basis desired; in Table IV four per cent compound interest is used, as more nearly representing the rate which should be applied to forest-property carrying charges and which may be more generally used in the future.

The "immediate-conversion values" in Tables III–IV were secured by applying to the timber stand what was believed to be fair stumpage rates for each tract. These rates represented an approximate five-year average for the period 1926–30. They are for early conversion or liquidation, i.e. within one to three years, when additional carrying charges are a small item. They are higher than are admitted equitable by most owners and lower than would be used by the chronic critics of private timberland exploitation. They are not listed at this time simply because they would in turn call for considerable space in their justification before extremists of either viewpoint.

The low range and the low average of immediate conversion value per acre will occasion some comment, but it should be remembered that:

1. The average stand per acre (tract run) is small, and 37 per cent of the sawtimber is hemlock. See Table I.

2. For immediate conversion many of the products listed actually have zero stumpage values on portions or all of a given tract, thus lowering the average positive values ascribed to them.

3. The values given are presumably net cash, with no operating or other risk.

4. There is now no positive residual land value. The stumpage values have assumed clear-cutting of all merchantable material. At the present time a very large proportion of the clear-cut lands is being abandoned by their owners upon the completion of cutting. Of those retained it is generally conceded that the average cost of taxes until sale is made, plus cost of selling and delivering title, plus frequent failure to complete payment, with litigation or loss, exceeds the average realized sale price. No possible positive value can be shown through holding *clear-cut* lands for timber production, under either the Pearson Act or the General Property Tax.

As previously indicated, the values arrived at in Tables III–IV are believed to be defensible as representing average conditions. If, however, we should arbitrarily double the conversion values, only three of the eleven tracts would show a figure greater than the accumulated cost in Table III, whereas in the four-per-cent table, five of the eleven tracts would still have negative values. It may be noted that these properties either have been carried for a very long period, about twenty-five years, or were purchased during the peak-price period, 1918-22, either of which results in high cumulative carrying charges. This situation is, however, quite typical of this region and elsewhere. In fact, some of the largest timber holdings in the state, not included in this group, have been held for a still longer time. In such cases even nominal purchase price and early tax payments accumulate to a large figure if compound interest and any reasonable rate are used. This whole situation emphasizes the position which has always been taken in general by foresters; that holding large bodies of merchantable timber can be justified financially only during periods of rising stumpage values or as costly "insurance," and that the

TABLE IV

Relationship of Accumulated Costs (4 per cent Compound Interest) to 1930, Inclusive, to the Immediate-Conversion Values of Eleven Merchantable Timber Tracts in the Upper Peninsula of Michigan

Tract no.	Year purchased	Per Acre									
		Four per cent			Four per cent			Total cost	Immediate-conversion value	Difference cost and value	Per cent Tax and Int. of conversion value
		Price	Int.	Total	Taxes	Int.	Total				
1	1903	3.26	5.43	8.69	7.74	4.57	12.31	21.00	13.76	− 7.24	89.5
2	1905	10.00	16.66	26.66	24.92	12.52	37.44	64.10	20.70	− 43.40	180.9
3	1906	11.45	17.90	29.35	16.99	6.38	23.37	52.72	21.79	− 30.93	107.4
4	1906	6.76	10.87	17.63	13.07	5.38	18.45	36.08	22.45	− 13.63	82.2
5	1918	10.81	6.51	17.32	12.25	3.17	15.42	32.74	17.87	− 14.87	86.5
6	1919	41.00	22.10	63.10	11.67	3.89	15.56	78.66	24.48	− 54.18	63.5
7	1920	7.72	3.70	11.42	3.93	0.85	4.78	16.20	13.15	− 3.05	36.4
8	1920	17.50	8.40	25.90	7.86	1.55	9.41	35.31	38.66	+ 3.35	24.4
9	1920	33.48	16.12	49.60	7.13	1.67	8.80	58.40	16.71	− 41.69	52.6
10	1921	23.07	9.78	32.85	6.46	1.28	7.74	40.59	17.08	− 23.51	45.3
11	1921	31.85	13.45	45.30	6.13	2.06	8.19	53.49	55.00	+ 1.51	14.9
Av. not weighted				29.81+			14.68+	44.48	23.79	− 20.69	71.2

proper set-up is a well-regulated forest (uniform distribution of age-classes with minimum investment in high-value mature timber) with a going wood-production business and sustained annual income. However, our problem here is to analyze the situation in which these owners actually find themselves; and we must admit that it is not a brief or simple task to convert our average forest property into the ideal set-up, all factors considered.

ANALYSIS OF "TAX RATES"

Though we have seen in Table II and Chart 1 (Fig. 46) the extent to which taxes have increased since 1905, it is obvious that a comparison of the tax with the "value" of the property gives a better conception of the tax burden; this is the usual manner of arriving at "tax rates."

For this purpose we may study Tracts 1–12 and 16 of Table II. For this group the average tax per acre for the five-year period 1926–30 was $0.91, and the average immediate-conversion value is $24.02 per acre, giving a rate of 3.79 per cent, or 38 mills per dollar.

The annual tax burden as represented by the figure 3.79 per cent of immediate-conversion value is fairly comparable with that commonly arrived at by the usual methods of taxation wherein merchantable timber-bearing land is treated in the same manner as are most other classes of real property. Further analysis shows, however, that under the normal conditions of ownership and exploitation of merchantable timber in Michigan the actual net cash values per acre are, primarily because of the time element, very materially less than these so-called immediate-conversion values. A true picture of the tax burden which will actually be borne (average) by these properties shows that it will greatly exceed the average annual rate of 3.79 per cent of assumed value.

If we make the fair assumption that the *average* of these thirteen properties will be liquidated through exploitation in a ten-year period, it is then possible to arrive at the "present worth" of the average acre which is valued at $24.02 for immediate conversion. If we use the tax of $0.91 per acre per year on the timberland and drop the land as cut over to avoid expense, and use 6 per cent as the interest rate, the present worth of the ten annual cuts is

$13.71 per acre. Applying this value we find the $0.91 per acre annual tax is actually 6.64 per cent of the realized value of the property.

Let us consider Tract 1 of Table II. This is the exceptionally large property, with a stand less than the general average. It would be readily acknowledged that it could not be practically liquidated through exploitation in less than fifteen years from 1932 without great waste, and the period is liable to be considerably longer. On an average per acre basis, the present worth of the fifteen-year cut is $6.03 per acre, instead of the immediate-conversion value, $13.76 per acre. Assuming our figures as conservative in this case and applying the five-year average tax of $0.49 per acre, we find that the annual tax burden is 8.13 per cent of the $6.03 present-worth value of the property, instead of 3.56 per cent as arrived at by the usual methods of tax-burden computation, by the $13.76 per acre valuation. An excellent check upon these figures is available. For several years the owner has had the property on the market at a figure of *$5.66 per acre;* and the $0.49 per acre tax represents 8.66 per cent of this offered sale price. There have been no buyers, and in 1931 the per acre tax jumped to $0.62, or 10.95 per cent of the offered price. Table V summarizes the situation with respect to this property:

TABLE V

TRACT 1, SHOWING VARYING TAX RATES DEPENDENT UPON METHOD OF VALUATION AND TAX LEVY

Method of valuation	Value per acre	Tax per acre	Tax rate
Immediate-conversion value.	$13.76	$0.49	3.56%
Present worth (15-year cut)..	6.03	0.49	8.13%
Offered price.....	5.66	0.49	8.66%
Offered price.....	5.66	0.62	10.95%
Immediate-conversion value.	13.76	0.62 (1931)	4.51%
Township assessor.....	12.67	0.62	4.88%

The similarity will be noted between immediate-conversion value and the township-assessed values, and between present-

worth and the offered-price values. Examination of Table III indicates that Tract 1 is far from being in the worst net financial condition of the group; if space permitted this could be shown by further analysis of individual tracts.

Chart 2 (Fig. 47) gives graphically for each of the thirteen tracts held in 1930 the immediate-conversion stumpage values

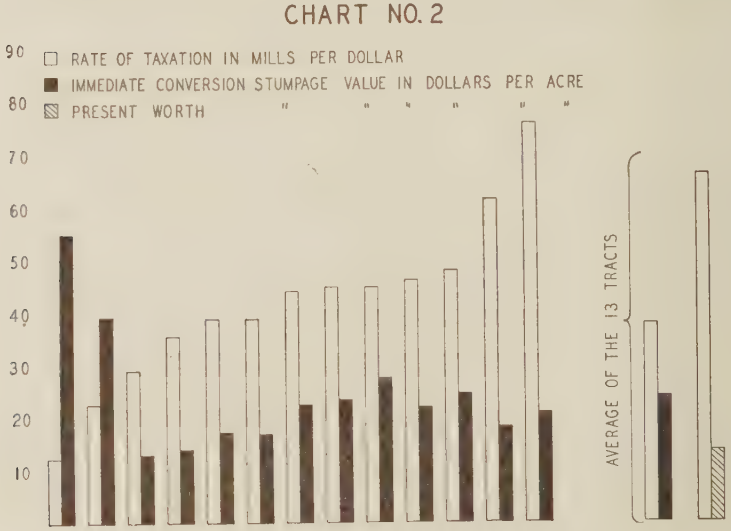


FIGURE 47

per acre, and the rate of taxation in 1930 in per cent of this conversion value, together with the average for the thirteen properties on the basis of immediate-conversion value contrasted with present-worth value.

Chart 3 (Fig. 48) shows graphically the stumpage values and tax rates for Tract 1 under various methods of valuation.

SUMMARY

Though the analysis herein presented is not exhaustive, it would seem to indicate rather clearly that under our present system of timberland taxation in Michigan:

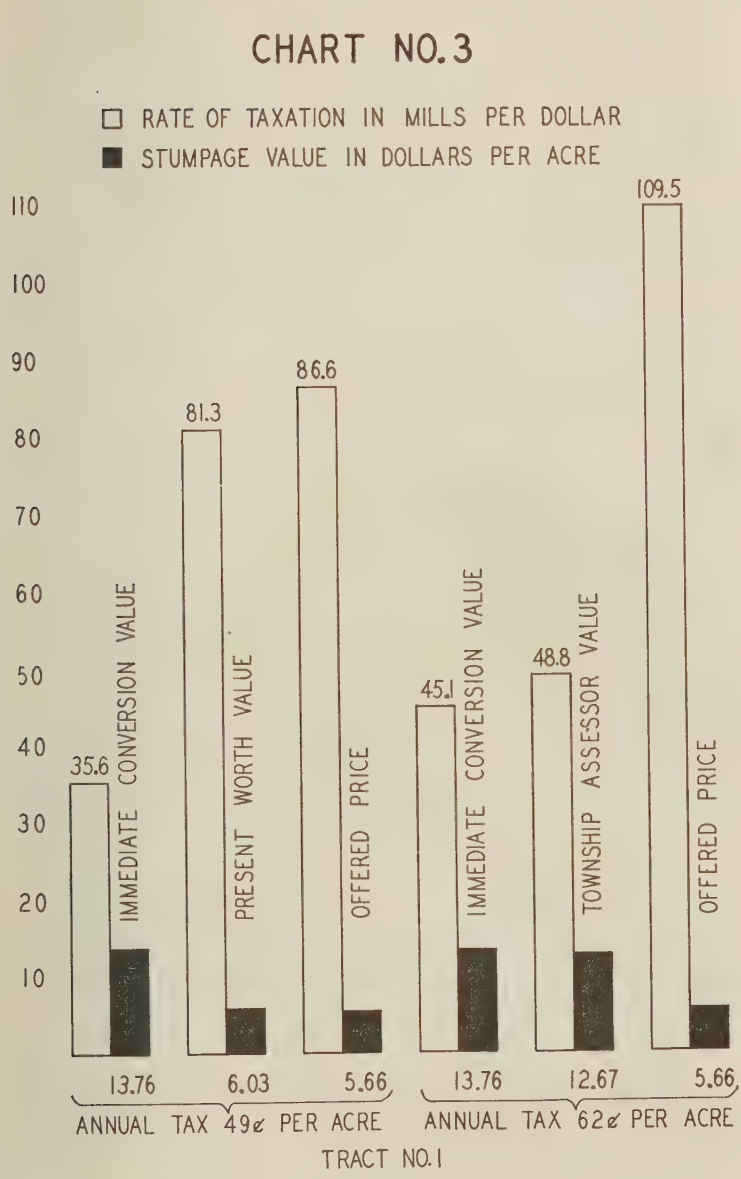


CHART NO. 3
RATE OF TAXATION IN MILLS PER DOLLAR
STUMPAGE VALUE IN DOLLARS PER ACRE
110
100
90
80
70
60
50
40
30
20
10
35.6
81.3
86.6
45.1
48.8
109.5
IMMEDIATE CONVERSION VALUE
PRESENT WORTH VALUE
OFFERED PRICE
IMMEDIATE CONVERSION VALUE
TOWNSHIP ASSESSOR VALUE
OFFERED PRICE
13.76
6.03
5.66
13.76
12.67
5.66
ANNUAL TAX 49¢ PER ACRE
ANNUAL TAX 62¢ PER ACRE
TRACT NO. 1

FIGURE 48

1. Taxes are a very important item in carrying charges and may frequently be the deciding factor in dictating liquidation.

2. Taxes in terms of percentage of valuation arrived at under any given system of valuation vary widely for individual tracts or ownerships, particularly by political townships.

3. Taxes have increased tremendously since 1906 and for the properties studied were in 1930 at an average rate which approximates 6.64 per cent of the capital value of the property each year.

4. In the absence of any present or probable early stumpage-value increment, this amounts in the average mature forest to a yearly and consequently pyramiding annual depreciation charge. (If the forest is in good growing condition this may be offset by about two to four per cent.)

5. Unless other sources of appreciable income (recreation, fur farming, etc.) can be developed on the average property, early liquidation of the *major* timber values is the only sound financial policy. (With the better stands, selective or partial logging and listing under the Pearson Act are strongly recommended for consideration.)

If the tracts of timber here presented are at all representative, there is urgent need for a more scientific and equitable method of taxation, if we are to forestall wholesale liquidation and land abandonment at the earliest opportunity of the average owner. Any solution to be permanently satisfactory must take into account the sustained earning power of the property. Of these methods there may be suggested for consideration (1) the taxation of present worth as determined by capitalizing current income, as presented by Professor D. M. Matthews, School of Forestry and Conservation, University of Michigan, in his manuscript "Tentative Suggestions for the Valuation of Forest Property under the General Property Tax," October, 1931, and (2) legislation somewhat similar to the Rushton Bill proposed in the 1930 legislature of Michigan.[1]

University of Michigan

[1] Senate Bill No. 72. Michigan Legislature, Senate. Journal of Senate of 56th Legislature.

RECENT DEVELOPMENTS IN THE TYPES AND USES OF PUMPING EQUIPMENT IN FOREST-FIRE SUPPRESSION

GILBERT STEWART

INTRODUCTION

METHODS used in suppressing forest fires have improved greatly in recent years. The last decade has brought about the widespread use of motor trucks and of tractors equipped with suitable plows. Specialized types of pack-sack pumps have been perfected, and power-pumping equipment has been developed.

These relatively new devices have made it possible to employ direct methods of attack on fire fronts and have replaced, in many cases, the ever ready back-firing torch. The use of power-pumping equipment has barely started, and it is with this type of equipment that the following paper is concerned.

TYPES OF PUMPS AVAILABLE

A number of pumps have been designed especially for use in forest-fire suppression. They differ in principle and might be classified simply into two groups. Positive displacement pumps include all rotary, piston, and plunger units. Non-displacement pumps include all centrifugal units.

For use in woods work it is essential that power pumps be driven by gas engines.

Rotary pumps consist of a shell or cover in which the rotating parts are contained. The pumping action is developed by the rapid rotation of the rotors within the shell. The rotors themselves consist of slotted cylinders or else gears. Suction is produced behind the slots, and water is thereby drawn into the shell. The rotation of the working parts, at the same time, causes a compressing action or displacement of that water which is caught

ahead of the slots or gears, and it is forced out of the discharge vent.

Most rotary pumps are connected directly with the engine driving them, and their speed of rotation is identical with that of the engine.

Piston pumps consist of one or more cylinders in which pistons travel back and forth. The movement of a piston creates suction behind it, and water is therefore drawn into the cylinder. The cylinder acts as a compression chamber when the direction of the piston is reversed. Valves are properly timed to permit the intake of water into the compression chamber and the outlet of water into the discharge vent.

Piston pumps are termed "single-acting" if water is drawn and discharged at one end of the piston only; they are called "double-acting" if each oscillation of the piston causes both intake and discharge. Double-acting pumps are preferred because of greater capacity and the elimination of excessive pulsation in the hose line.

Piston pumps are always driven at relatively slow speeds. They are geared down, and the engine speed is usually three or four times that of the pump.

Plunger pumps are very similar to piston pumps in mechanical design and action. They differ in that plungers are usually made to travel vertically, whereas piston pumps work horizontally. Plunger units are commonly mounted with three working plungers, in which case they are called "triplex." Like piston pumps they operate at slow speed.

Centrifugal pumps are non-displacement pumps. They attain their pumping action by means of the rapid rotation of an impeller within a shell. Suction is created behind the blades of the impeller, which draws water into the shell. The discharge from the shell is caused by the throwing of the water centrifugally from the ends of the impeller blades.

ADVANTAGES AND DISADVANTAGES OF EACH TYPE

Each type of pump has certain advantages which recommend it for use; likewise certain disadvantages limit the use to which it can be put.

Rotary pumps have the ability to develop high pressure and adequate volume, even when built in small sizes. They are compact and light and, when coupled with specially designed engines, permit easy transportation. They are always self-priming.

Serious disadvantages, however, are inherent in the pumps. They depend upon exceedingly close machining between the rotors and the shell. If this small tolerance is destroyed by grit and sand, the pumps are quickly ruined and are rendered useless until new rotors are installed. This is a major repair and cannot be made in the woods. Furthermore, rotors are expensive.

Rotary pumps require relatively high speeds for maximum efficiency. Types and sizes suitable for woods work require at least 2,000 revolutions per minute; a speed of 2,500 revolutions is preferable. Such speeds are frequently abusive, considering the lightweight engines that are used to drive the pumps. The result is that such power units are short-lived and often unreliable in performance.

Piston pumps possess the advantage of simplicity in design. In service they are absolutely dependable, and the mechanism cannot be easily harmed. The wearing internal parts are usually leather cups. They are subject to wear when sand or grit is pumped, but the pump is not put out of commission if subjected to such abuse. Owing to the design and construction of piston pumps they permit easy repair and replacement of parts in the woods. Repair parts themselves are very cheap.

Inasmuch as piston pumps are driven at slow speeds, the engines used to drive them are not subject to excessive racing. Powerful engines rather than fast ones are needed, and it is not essential that their speeds exceed 800 revolutions per minute.

Owing to the dependability and simplicity of piston units small crews may be used to operate them. After a pump is in position for use, one man can operate both the engine and the hose line. Two men constitute a very efficient crew, and never more than three are needed.

The only disadvantage of the piston unit is weight. Not many of them are made light enough to be carried by fewer than four men. However, this difficulty may be overcome by mounting

the entire unit on an efficient trailer, suitable for towing by car, tractor, or team.

Field experience of the past year proves that when correctly mounted, such units may be taken into rough and almost inaccessible country. They are by far the most reliable pumps that have been put into fire service throughout the state.

Plunger pumps are so nearly like the piston units that their advantages and disadvantages are approximately the same. They have not yet been supplied in large numbers for forest-fire service. In actual service they ought to prove as reliable as the piston pumps.

Centrifugal pumps possess the advantage of simplicity in design and construction, with few working parts. Most of them are small, compact, and light, and may be coupled with engines of a number of types. Such pumps may be used in locations where sandy and dirty water prevails. Grit has little effect upon the working parts, since close machining and small tolerance are not essential to induce suction.

The chief disadvantage of the centrifugal pump is that it cannot produce high pressures, unless it is specially designed for that purposed. High impeller speeds are needed for building pressure. These may be secured by the use of high-speed engines, or through the use of gearing within a gear box. Recently a small, self-priming, geared centrifugal pump has been perfected; equipment of this kind marks a great advance in the design of pumping units. It is small, light, capable of high pressure and capacity, and in service has proved to be very reliable. In this particular pump high impeller speeds are secured by a gear ratio of 4 to 1. It is powered by a high-speed gas engine capable of 3,000 revolutions per minute.

HISTORY OF THE USE OF PUMPING EQUIPMENT

Power pumps have been used in forest-fire suppression since 1923. At that time the first pumps were placed on the market, designed especially for woods work. By 1927 a number of manufacturers were offering lightweight fire-fighting units. All the first types were designed to reduce weight to a minimum. High-

speed marine motors were used for producing power, and the pumps were all rotaries.

When tested in service they left much to be desired; engine performance was decidedly temperamental and unreliable; the rotary pumps deteriorated rapidly from the effects of sand. Troubles of this sort have persisted to the present time, especially with those units employing two-cycle motors.

Manufacturers of centrifugal units attempted to supply reliable pumps not subject to excessive wear. Some success was attained, but they were still limited largely to two-cycle motors, and the single-stage centrifugal pumps which they supplied could not build sufficient pressure to operate long hose lines.

The fire seasons of 1930 and 1931 presented favorable opportunities for field tests of the latest types of pumping equipment. Complete tests of seven leading types of pumps were conducted at the Michigan Forest Fire Experiment Station. These tests were controlled to determine the performance of the various units for pressure and capacity, and their ability to operate long hose lines.

In addition, the pumps were tested on actual fire and subjected to the same treatment that regularly assigned pumps are expected to withstand. It was during these tests that the superiority of heavy-duty pumps became apparent. The high-speed light pumps frequently failed in service; the slower, heavy-duty pumps remained in daily operation for weeks at a time without experiencing difficulty. One heavy-duty rotary pump, however, ground out two sets of rotors.

USE OF PUMPING EQUIPMENT ON FIRE

Like all specialized equipment, power pumps are restricted to particular uses and situations. The chief limiting factor is that imposed by the available water supply. Pumps are especially adapted to regions plentifully supplied with lakes and streams, but are less suited to those locations where water is scarce and the operation of long hose lines necessary. Many of the present types of pumps are unable to operate 3,000 feet of hose, and few pumps may be expected to perform efficiently beyond 5,000 feet. The

best use of pumping equipment is realized when relatively short hose lines can be operated; it is desirable to restrict them to 1,500 feet or less.

In actual use pumps are effective weapons with which to suppress fires. They make direct attack possible, and all fires within reach of the hose stream may be completely killed. No other method of attack is so efficient in this respect. When properly used, pumping equipment permits dangerous fronts to be extinguished, and hot, fast-running fires may be stopped at roads, fire lines, or natural breaks.

In the case of peat fires pumps provide the most satisfactory means of attack yet discovered. These are slow-running fires that burn deep under ground and must be flooded to be put out. With pumps such fires may be controlled while small. Plowed furrows are only partly successful, and small hand pumps fail completely in fighting peat fires. A large volume of water, delivered at fairly high pressures, is required, and power pumps are the only means by which this may be secured.

Past experience indicates that, in the use of pumping equipment, one serious problem must be solved, namely, that of laying hose. In cases where fire spreads faster than it can be pumped out and additional hose laid, one single pump cannot be depended upon to stop it. More pumps are then required, or some other method of stopping the running head must be employed. This situation is solved in some degree by using large units capable of great capacity and high pressure, so that two or more outlets may be taken from one main hose line.

PUMPING FROM WELLS

The most serious limitation in the use of pumping equipment is absence of a water supply adjacent to fire. The problem can be solved, in some instances, by means of wells to supply water to the pumps.

During 1931 experiments were conducted at the Michigan Forest Fire Experiment Station to determine the feasibility of pumping from wells. Series of test wells were located, covering a range of depths of the water table. Pumping tests were carried

out with pumps of high capacity. These tests were exceedingly successful. It was found that large pumps could be fully supplied by well points connected in series. Furthermore, no test well could be exhausted, and in every case all improved with continued pumping. Several wells yielded more water per minute at the termination of the tests than they had produced at the start. These tests covered several hours; one particular well supplied a large pump over a period of four hours and yielded an unimpaired flow of 5,800 gallons.

Investigations were also started to discover ways of sinking well points rapidly. Ordinary driving or digging is too laborious and time-consuming. One method of jetting has been developed, whereby points may be placed beneath the water table very rapidly. One large well point was washed to the water table at a depth of nine feet. The time required to set the point in place was less than a minute, and the well yielded a flow of water six minutes after the start of operations.

The research work involved in placing the points beneath the water table is not yet completed. It will be continued until a method is developed whereby well points may be placed in position for pumping quickly and efficiently.

FUTURE OF PUMPING EQUIPMENT

Power pumps are certain to be widely used in woods work, especially in districts where water is abundant. In all probability power pumping will not fulfill its greatest usefulness when used alone. Its greatest value lies in supplementing other fire-fighting tactics.

For instance, tractors and plows constitute the best possible means of constructing fire lines around running fire, and thereby stopping it; however, they furnish no way of direct attack upon the fire. Pumps, on the other hand, are effective in direct suppression, but are limited in the speed with which hose may be laid, and cannot always head off fast-running fire. The two methods used jointly promise to be exceedingly efficient, since the pumps can be used to "mop up" fire encircled by the plow lines. These

tactics ought to prove valuable in holding hazardous points, especially in thick cover and slash.

Pumps also make back-firing possible where plow lines cannot be constructed or where highly inflammable cover exists. The front along which the back-fires are to be set may be thoroughly wet down beforehand, and the back-fires started under the protection of the hose lines.

Well pumping is thoroughly practicable and will broaden the scope of such equipment. This is especially important in the case of peat and swamp fires, inasmuch as water tables are high in such locations, and the underground water supplies are readily available. Short hose lines may be used, and the fullest efficiency of the pumps can be attained. All highland areas where the water table is within twenty-two feet of the surface offer the possibility of well pumping.

Two conditions, only, limit the possibility of well pumping: rock layers, naturally, prevent the sinking of well points; and impervious soils, such as clay or heavy silts, yield little or no water, even though the water tables in these soils may be within reach of a suction pump.

Test pumping has shown that a series of five common well points properly located with reference to one another are capable of supplying full capacity to heavy-duty pumps, whereas three points are sufficient for smaller ones. Investigations now under way are determining the feasibility of using high-efficiency well screens, and it is probable that screens as large as three inches in diameter may be used. If this proves to be the case, one point only will be needed to supply full capacity to the larger types of pumps.

The fact that well pumping is practicable opens up new possibilities in the protection of areas of high value such as game refuges and sanctuaries, parks, and estates. On such properties wells may be permanently located at strategic points, and need not be closer to one another than 3,000 feet. The cost of installation of such equipment is not prohibitive, and the wells would be serviceable over a period of years.

DESCRIPTION OF THE PUMPING UNITS TESTED

All pumps perform most satisfactorily when operated at the speed for which they were designed. Units may be driven at speeds faster than that which is deemed correct, but such operation is actual abuse, and no pump can be expected to perform satisfactorily for long periods if subjected to racing speeds. This principle is so well established that certain units are provided with automatic governors which fix the limit for maximum operating speed.

Seven pumping units have been tested to date. The tests to which they were subjected were held uniform throughout, so that the resulting data serve to compare the pumps on a basis of performance. The pumps tested are as follows:

1. *Pacific Marine Pump — Type N*

The Type N pump is a small, compact unit; the total weight is 70 pounds. It may be carried by one man, and is capable of operating a main line of large hose. Capacity is not great enough to warrant the use of more than one nozzle outlet.

Power is supplied by a four-cylinder, two-cycle, marine motor of the opposed type. The pump is a geared rotary, and is coupled directly with the engine, so that speeds are identical. In spite of the small size considerable power is developed. The correct operating speed is 2,500 revolutions per minute, but racing speeds of 3,000 revolutions and more are possible.

In field tests the Type N pump has not proved satisfactory if used for long, continuous periods. Engine failure is frequent; cylinder-head parts melt because of the intense heat developed within the motor. The unit appears to be overpowered for its size and weight, and must be well cared for. A pump man must be in attendance at all times.

2. *Pacific Marine Pump — Type K*

The Type K unit is a small portable outfit weighing about 150 pounds. It is designed for use in country where transportation is difficult and lightweight equipment must be used.

Power is provided by a two-cylinder, two-cycle marine motor

of the opposed type. The pump is a geared rotary; pump and motor are coupled direct, so that the speeds are identical. Correct operating speed with this unit is 2,500 revolutions per minute.

In test the Type K pump proved to be the most satisfactory of all the portable pumps. It is a well-balanced unit in which the pump and engine are correctly matched. It is capable of handling long hose lines, even when two nozzles are used. The cost of operation is high.

3. *Pacific Marine Pump — Type P*

The Type P pump is the largest hand-portable unit now on the market. It is powered by a large, four-cylinder marine motor of the opposed type. It is a two-cycle, high-speed motor.

The pump is a geared rotary of large capacity; pump and engine speeds are the same, since they are coupled directly. The correct operating speed is 2,500 revolutions per minute.

The Type P pump, which is a unit of great power, has the greatest capacity of any marine pump now available for forest-fire duty. High pressures are attainable, and two lines must be taken from the pump when it is operated at correct speed. The capacity, under proper running conditions, is 5,100 gallons per hour. Capacities of 100 gallons or more per minute are available when the motor is raced.

Under test this unit proved to be erratic; it is difficult to start, owing to the compression developed in the four large cylinders. The designers have attempted to combine lightness with power; they succeeded in attaining both, but it is probable that the unit will have a short operating life inasmuch as it is light and is subjected to high speeds. During the tests failures developed because of broken parts and faulty ignition. The operating costs are high — about four times as great as those of the Fairbanks pump.

The Type P pump is capable of supplying two main lines and four nozzle outlets. It may be easily carried by two men.

4. *Novo Pump*

The Novo pump is an assembled unit. The engine is a standard Novo two-cylinder, four-cycle gas engine. The pump coupled

with it is a Northern rotary of the geared type. The whole unit is a heavy-duty outfit and is transported on a two-wheel trailer. The weight is approximately 700 pounds.

The motor develops ten horsepower, and the engine speeds are controlled by a governor which prevents operation in excess of 1,250 revolutions per minute. The pump is coupled directly with the motor.

The Novo pump contains one feature which is a marked improvement in the design of pumping units. The pump is controlled by an outside clutch, which permits the power to be disengaged from the pump shaft; the engine may be permitted to idle while the pump is stationary.

In the original assembly the Novo unit was coupled with a Viking rotary pump similar to those used on the Kohler and Evinrude machines. However, in actual service the rotors were ruined so quickly by grit that another type of pump had to be used in place of the Viking.

In test and actual service the Novo pump has proved to be absolutely reliable. It may be left to itself, and will run for a period of three hours without attention; in emergencies one man can operate both pump and hose line.

The chief disadvantage is weight, although the unit is well mounted on a trailer and may be easily towed by car or team.

5. *Fairbanks-Morse Piston Pump — Model Z*

The Fairbanks-Morse pump is a heavy-duty unit weighing approximately 750 pounds. It must be mounted on a truck or trailer to be transported.

The engine is a single-cylinder, horizontal-acting gas engine; its rated horsepower is five. Actually it develops about six horsepower. The operating speed is 650 revolutions per minute.

The pump is a double-acting, two-cylinder piston pump. The length of the stroke is two and one-half inches, and the diameter of the bore two and one-half inches. It is driven by a system of multiple belts, at a speed of 215 revolutions per minute; the pulley ratio is therefore three to one.

The rated capacity is 2,500 gallons per hour, and the maximum

pressure is stated at 100 pounds. This is conservative. In actual test the unit delivered a maximum of 2,800 gallons per hour, and developed a pressure of 175 pounds on the hose line.

In all tests the Fairbanks pump proved to be exceedingly satisfactory and reliable. Its only disadvantage is weight. The unit is simple to operate, and the costs of operation are low.

6. *Kohler Water Pumper — Model WP–35*

The Kohler pump is a medium-sized unit weighing 300 pounds. It is an assembled unit; the motor is a standard Kohler four-cycle engine of four and one-half horsepower; the pump is a Viking rotary.

The engine is exceedingly reliable and satisfactory in operation; it is similar to an automobile engine with oil-base type of lubrication. The constant attention of the operator is not necessary; the unit may be left unattended for several hours at a time and, consequently, one man may operate both pump and hose line.

The maximum safe running speed is 1,500 revolutions per minute. The pump is coupled directly with the engine and their speeds are identical. The capacity and pressure developed by this pump are sufficient to operate one main hose line and one nozzle outlet.

The pump with which this unit is provided cannot be considered a sturdy and reliable one for field use. It is subject to fast deterioration where sand is encountered. When used to pump water that is perfectly free from sand or fine grit, it is satisfactory and efficient, but undue care in this respect cannot always be taken.

7. *Evinrude Pump — Model DDV*

The Evinrude pump was one of the first successful units used in fighting forest fire. It is powered by an Evinrude two-cycle, marine motor; the cylinders lie in line, and the engine differs from the Pacific Marine motors in this respect. The engine is rated at five horsepower.

The pump is a Viking rotary similar to the one used with the Kohler pump, but is of a smaller size. It is mounted integral with the motor. The correct operating speed is 2,000 revolutions per minute.

In field tests, conducted with a number of these pumps, serious faults have developed. The construction is light, and all working parts are made as small as possible. Burned-out connecting rods constitute a common failure. Back-firing has sheared off the flywheel in several cases, and sand-scored rotors are the usual occurrence.

Compared with other pumping units this is an obsolete model, although the capacities and pressures developed are greater than with some other pumps of more improved design.

BASIS OF COMPARATIVE TESTS

Experience proves that all pumping units should be operated at speeds well below the maximum of which they are capable; to drive them at racing speed reduces the working life, and causes frequent breakdown. Designers of pumps are accustomed to set a limit which they term the "maximum safe speed" or the "correct speed."

The usefulness of a unit is determined by its performance on a hose line when operated at its correct speed. The tests conducted with the pumps described above were based on correct operating speeds, and the performances of the several units were measured in terms of capacity and pressure when hose lines of increasing length were coupled with them. During the tests operating speeds were held constant by means of a tachometer; pump pressures were determined with an accurate test gauge, and capacities were measured by catching the discharge in graduated tanks.

The data secured are presented in the accompanying figures (49–50) and tables.

ANALYSIS OF THE DATA

The curves of pressure and capacity illustrate to good advantage the performances of the pumps. It is obvious that the results secured with the Novo pump are at variance with those obtained with the other units. The fall-off in both pressure and capacity is due to a rapid loss in engine speed after the unit has developed its maximum power. All hose line added beyond that point constitutes an overload which cannot be taken care of. As it

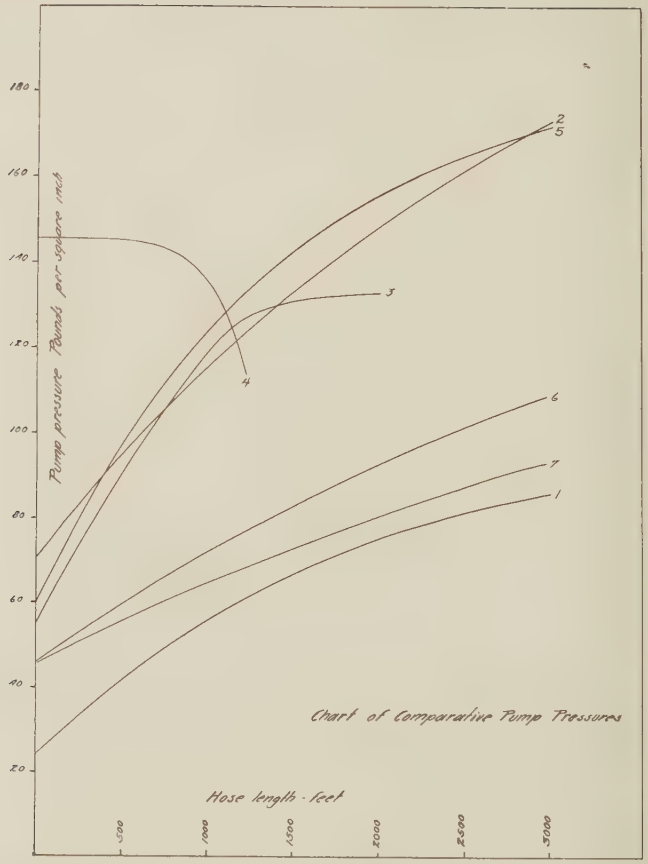


FIG. 49. Comparative pressure tests, showing the pressures developed by the various units when operated at the correct speeds. The same hose hook-up was used in all cases. Main line of 1½-inch hose with one outlet at the end of the hose line. Nozzle orifice $\frac{15}{32}$ inch

Explanation of curves: 1, Pacific Marine, Type N; 2, Pacific Marine, Type K; 3, Pacific Marine, Type P, two lines; 4, Novo; 5, Fairbanks-Morse, Model Z; 6, Kohler, WP–35; 7, Evinrude, Model DDV

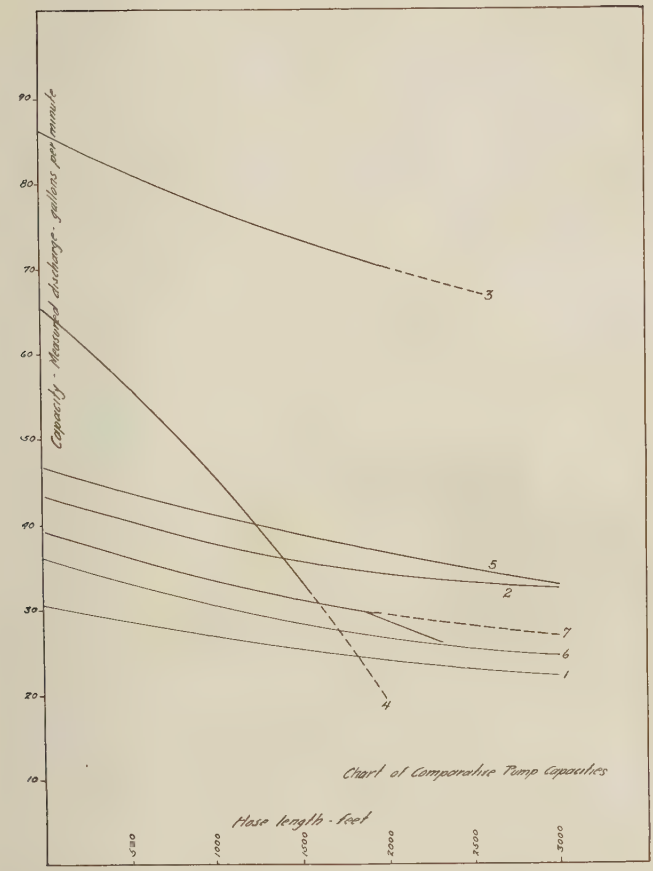


FIG. 50. Comparative capacity tests, showing the capacities available with the different units when operated at the correct speeds. The same hose hook-up was used in all cases. Main line of $1\frac{1}{2}$-inch hose with one outlet at the end of the hose line. Nozzle orifice $\frac{15}{32}$ inch

Explanation of curves: 1, Pacific Marine, Type N; 2, Pacific Marine, Type K; 3, Pacific Marine, Type P, two lines; 4, Novo; 5, Fairbanks-Morse, Model Z; 6, Kohler, WP–35; 7, Evinrude, Model DDV

is now assembled, the unit suffers from bad balance between available engine power and the power required to drive the pump. It should be restricted to operating hose lines under 1,000 feet in length.

The capacity curve of the Evinrude pump shows that an abrupt decrease in discharge occurs when the hose line is extended beyond 1,800 feet. This is due to the fact that the maximum engine power has been attained, and all hose added thereafter constitutes an overload.

All the curves show that there is a regular and uniform decrease in discharge as length is added to the hose line. This is due to the increased load and the weight of the water core carried by each additional hose section, as it is coupled into the line. This is also reflected in the pressure curves; increased water load in the hose lines causes a corresponding increase in pump pressure. Actual water load is the sum of the weight of the water and the internal friction developed between the water column and the inner wall of the hose.

CONCLUSIONS

The investigations to date permit a number of conclusions with reference to pumping equipment and its use:

1. Portability is not the most important feature to stress in the design of pumping equipment. This holds true for all units except those used in the most isolated and inaccessible country.
2. Reliability and sturdiness are features more desirable than portability.
3. Heavy-duty units, when properly mounted on efficient trailers, may be taken wherever cars, tractors, or teams are able to go.
4. Owing to mechanical design and construction piston, plunger, and centrifugal pumps are to be preferred to rotary pumps.
5. Rotary pumps are highly efficient and useful where clean water is available. They lend themselves readily to small, light units in which portability is the most desired feature.

TABLE I

COMPARATIVE PRESSURES DEVELOPED BY THE PUMPS WITH INCREASE IN LENGTH OF HOSE LINE

All units operated at their correct speeds. Hose hook-up: main line of $1\frac{1}{2}$ inch hose; one nozzle outlet; nozzle orifice $\frac{15}{32}$ inch

Hose length in feet	Pacific Marine Type N	Pacific Marine Type K	Pacific Marine Type P	Novo	Fairbanks-Morse Model Z	Kohler Model WP-35	Evinrude Model DDV
	Values are pounds pressure per square inch						
100	28	76.5	62.5	146	67	49	46
200	32	81	69.5	146	75	51	48
300	35.5	86	77	146	82.5	54	51.5
400	38.5	90.5	83.5	146	89.5	56	53.5
500	42	95	90.5	145.5	96.5	59	55.5
600	45.5	99.5	97	145	102.5	61	57
700	48.5	103.5	103	144	108	64	59
800	51	108	109	142.5	113.5	66	61
900	54	112	114.5	140	118.75	69	62.5
1000	56.5	115.5	119.5	136	123	71	64.5
1100	58.5	119.5	124	129	128	74	66
1200	60.5	123	127.5	118	132	76	68
1300	63	126.5	129.5	....	136	78	69.5
1400	65	130	131	....	139.5	80	71
1500	66.5	133.5	132	....	143	82	73
1600	68.5	136.5	132.5	....	146	85	74.5
1700	70.5	139.5	133	....	149	87	76
1800	72	142.5	133.5	....	151.5	89	77.5
1900	73.5	145.5	134	....	154	91	79
2000	75	148.5	134	....	156.5	93	80.5
2100	76.5	151	....	....	158.5	95	81.5
2200	78	154	....	....	160.5	97	83
2300	79	156.5	....	....	162	99	...
2400	80	159	....	....	164	100	...
2500	81	161	....	....	165.5	102	...
2600	82	163.5	....	....	167	103	...
2700	83	166	....	....	168	105	...
2800	84	168	....	....	169.5	107	...
2900	85	170.5	....	....	170.5	108	...
3000	86	172.5	....	....	171.75	110	...

TABLE II

COMPARATIVE CAPACITIES DEVELOPED BY THE PUMPS WITH INCREASE IN LENGTH OF HOSE LINE

All units operated at their correct speeds. Hose hook-up: main line of $1\frac{1}{2}$ inch hose; one nozzle outlet; nozzle orifice $\frac{15}{32}$ inch

Hose length in feet	Pacific Marine Type N	Pacific Marine Type K	Pacific Marine Type P	Novo	Fairbanks-Morse Model Z	Kohler Model WP–35	Evinrude Model DDV
	Values are capacity in gallons per minute						
100	30.5	43	85	63.75	46.25	36	38.75
200	30	42.25	84	62	45.5	35.2	38.25
300	29.75	41.75	83	60.25	45	34.5	37.5
400	29.5	41.25	82.5	58.25	44.5	33.7	37
500	29.25	40.5	81.5	56.25	44	33	36.5
600	29	40	80.5	54.25	43.5	32.5	36
700	28.75	39.5	79.5	52.25	43	31.9	35.25
800	28.5	39.25	78.75	50.25	42.5	31.4	34.75
900	28.25	38.75	78	48.25	42	30.9	34.25
1000	28	38.25	77.25	46	41.5	30.5	33.75
1100	27.75	37.75	76.5	43.75	41.25	30.0	33.25
1200	27	37.25	75.75	41.5	40.75	29.6	32.75
1300	26.75	37	75	39	40.25	29.3	32.5
1400	26.5	36.5	74.25	36.5	39.75	28.9	32
1500	26.25	36.25	73.5	34	39.5	28.5	31.5
1600	25.75	35.75	73	....	39	28.3	31.25
1700	25.5	35.5	72.25	....	38.5	27.9	30.75
1800	25.25	35.25	71.5	....	38	27.6	30.5
1900	25	34.75	71	....	37.75	27.4	29.5
2000	24.75	34.5	70.5	....	37.25	27.3	28.75
2100	24.5	34.25	....	....	36.75	26.9	28.25
2200	24.25	34	....	....	36.25	26.6	27.5
2300	24	33.75	....	....	35.75	26.4	....
2400	23.75	33.75	....	....	35.5	26.3	....
2500	23.5	33.5	....	....	35	26.1	....
2600	23.25	33.25	....	....	34.5	25.9	....
2700	23	33.25	....	....	34.25	25.7	....
2800	22.75	33	....	....	33.75	25.5	....
2900	22.5	33	....	....	33.5	25.4	....
3000	22.25	32.75	....	....	33.5	25.3	....

6. Piston and plunger pumps of high capacity are not available in lightweight units.

7. All pumps suitable for use in forest-fire suppression must possess the ability to deliver volume and pressure. It is a mistake to go to extremes in either case. Extreme pressure is destructive to hose equipment. Volume, on the other hand, is of no use unless sufficient pressure is available to drive the water where it is needed.

A logical compromise is a maximum pressure of 180 pounds; all advantage over that should be in terms of volume.

8. Four-cycle motors are to be preferred to two-cycle motors; they are more reliable, less temperamental, and are easier to start and to operate. However, two-cycle engines may be made in smaller sizes and in much lighter weights than four-cycle motors and, in some instances, are more adaptable to lightweight units.

9. Well pumping is thoroughly practicable. The only limitations are that water must be available within twenty-two feet of the ground surface, and that it is contained in a pervious layer of soil.

Department of Conservation
Lansing, Michigan

LIVE-TRAPPING MICHIGAN WHITETAIL DEER

ILO H. BARTLETT

DURING the experiments in live-trapping and tagging of wild deer which have been conducted by the Game Division of the Michigan Department of Conservation, considerable information on the sex and age ratios, weights, physical condition, migrations, and general habits has been collected.

Trapping experiments were carried on in swamps where deer bunch up or "yard" during severe winters. The most intensive effort was made during the winter of 1930–31 in the Fletcher swamp in southwestern Alpena County. This experiment was performed in order to determine the feasibility and costs of live-trapping and removing deer from overcrowded areas.

At various times the United States Forest Service, the Wisconsin Conservation Department, and the Pennsylvania Board of Game Commissioners have live-trapped deer. The United States Forest Service has conducted the most extensive operations on the Kaibab National Forest and has caught as many as two hundred and ninety deer a season in corral traps placed around water holes.

For the past twenty-five years the Cleveland Cliffs Iron Company has used box traps twelve feet high to catch and remove as many as one hundred deer a year from their licensed game farm of 13,000 acres on Grand Island near Munising, Michigan.

Since the winter of 1928–29 the Michigan Department of Conservation has operated deer traps in various locations, but until the winter of 1930–31 no intensive effort was made to capture a large number of deer.

Starting in January, 1931, a trap at the Hulbert deeryard was operated sixty-two days. Eighty-seven catches were made involving twenty-nine different deer, or an average of 1.4 deer a

day. One deer was caught in a trap at Blaney and two were caught in traps at the Crawford Refuge during the same winter. They were liberated at the traps, and no attempt was made to transfer them to other localities.

From one to eight box traps were operated in the Fletcher swamp over a period of 74 days. During 255 "trap days" 129 catches were made, averaging approximately one deer a trap every two days. All the deer caught were tagged in the right ear with the standard Fritz ear tag used in marking cattle. The tags were numbered serially and stamped "Notify Dept. Cons. Lansing."

During the first few days of the experiment the eight deer which were caught and tagged were released again at the trap. Some of these "repeated" or were recaught from time to time until a total of fourteen repeat catches had been made. All the other deer caught were transferred in trucks and released in better yarding swamps. One deer, after being transferred $5\frac{1}{2}$ miles by truck and liberated in a swamp well supplied with feed and water, was recaught three days later in the same trap in the browsed-out swamp.

The only casualties due to trapping resulted when one deer jumped into the end of the trap and broke its neck and another just died, possibly from fright and exhaustion.

One hundred and nine deer were tagged during the winter. The ears of only four of these were injured, slightly, during the tagging operations.

The type of tag used seems well suited for this work, and in each of the thirteen cases when tagged deer have been reported the tag was securely attached and the ear appeared in excellent condition.

Some little trouble was experienced in finding locations suitable for the release of captured deer, but it is felt that all deer moved were placed in much better winter feeding territory than the Fletcher swamp.

The deer were transferred as follows:

11 deer 8 miles to the Wolf Creek swamp;
11 deer 45 miles to the Lunden State Game Refuge;
12 deer 22 miles to the Alpena State Forest;
65 deer 65 miles to the Iosco State Game Refuge.

In all, ninety-nine deer were transferred an average distance of 51.23 miles. The average cost for moving them was $1.59 per deer, or 3.1 cents a deer per mile. With the average trapping cost of $4.38 per deer, this makes a total of $5.97 for trapping and moving a deer approximately 50 miles.

The sex and age ratios among the trapped deer are interesting:

Total number 114: males 55 or 48.2 per cent, females 59 or 51.8 per cent;
Total number 114: fawns 74 or 65 per cent, adults 40 or 35 per cent;
Total adults 40: males 7 or 18.5 per cent, females 33 or 81.5 per cent;
Total fawns 74: males 48 or 64.9 per cent, females 26 or 35.1 per cent;
Total males 55: fawns 48 or 87.3 per cent, adults 7 or 12.7 per cent;
Total females 59: fawns 26 or 44 per cent, adults 33 or 56 per cent.

Weights among the trapped deer were as follows:

	Maximum	Minimum	Average
Males, adults.....	158 lb.	72 lb.	111.3 lb.
fawns.....	89 lb.	36 lb.	56.4 lb.
Females, adults....	125 lb.	59 lb.	108.9 lb.
fawns....	84 lb.	38 lb.	58.6 lb.

The deer were divided into the following groups, depending on their physical condition: 9 or 7.9 per cent, very good; 86 or 75.4 per cent, good; 12 or 10.5 per cent, fair; and 7 or 6.2 per cent, poor.

Casualties during the entire experiment totaled eleven, or a loss of 9.6 per cent of those handled. Two of these were lost by accidents in the traps, seven died in the holding pens, and two while being transferred.

The eleven deer that died during the experiment were sent for autopsy to Dr. Don Coburn, pathologist of the Michigan Department of Agriculture, at East Lansing. He reports that each was infested with from ten to eighty nosefly larvae (*Cephenomyia phobifer*), some as large as a lead pencil and over an inch long, and also with a species of lung worm (*Protostrongylus rufescens*). In the seven deer that died in the holding pens and the two that died in transit, the lung worms, which are almost microscopic, were so abundant that they had caused verminous pneumonia, which was given as the primary cause of death. In addition to the

two parasites mentioned before, two of the deer had stomach worms (Genus Ostertagia).

Important questions in connection with tagging are: "Where will deer go after being tagged? If transplanted to another locality do they tend to return, and, if so, from what distances?" These questions, of course, could be answered only through reports from year to year of the shooting or recapture of marked animals. Reports have been received concerning thirteen of the one hundred and fourteen tagged deer. The buck tagged at Blaney in January, 1930, was shot in November of the same year 14 miles from the trap where it had been tagged. Reports were received on two adult does caught and tagged in the Fletcher swamp in March, 1931, and released on the Iosco State Game Refuge near Oscoda, about 40 miles away. About a month later one was killed by an automobile $2\frac{1}{2}$ miles north from where it had been released; and the other was found dead in a woven wire fence two miles south of the point of liberation.

Two of the deer tagged at Hulbert in early April, 1931, were killed the following November. One had wandered 17 miles from the trap location and the other but one-half mile.

A deer marked at its winter yard in the Crawford Refuge in January, 1930, was shot in November, 1931, only 4 miles from the place where it had been caught and tagged nearly two years before.

During the 1931 deer-hunting season in November reports were sent in on seven of the forty-seven bucks which had been caught and tagged in the Fletcher swamp and liberated in various locations. One released in the Wolf Creek swamp, which is 5 miles east of the Fletcher swamp, was killed on the shore of Lake Huron 14 miles east of where it had been released nine months before, and 20 miles from where it was trapped. Another buck, released in March on the Lunden Refuge 15 miles west of the traps, was killed 3 miles east of where it was caught, or a distance of 18 miles from where it was liberated. Two bucks released in March, 22 miles away on the Alpena State Forest, were killed the following November one-half and one mile from where they had been set free. Three of the bucks released in March at the Iosco Refuge, 40 miles from the Fletcher swamp, were killed

in November. One was 6 miles west and two about 9 miles south of where they were released.

The record indicates that there were sixty-eight tagged bucks unaccounted for or roaming the woods of Michigan at the beginning of the 1931 deer-hunting season. Authentic reports were received that ten of these were killed during the fifteen-day hunting period. That is, 14.7 per cent or more of the tagged bucks were killed. This might be used as an index to estimate the percentage of the total buck population killed during the 1931 deer-hunting season.

Because of the comparatively small number of individuals handled and the small number of returns received the data gathered cannot be accepted as conclusive, but from the information available it seems that:

1. It is practicable to trap deer on a large scale in congested deeryards.
2. The deer thus trapped can easily be tagged, and the tag has no harmful effects.
3. Deer trapped in overbrowsed winter yards can be economically transferred to better cover and feed areas.
4. The sex and age ratios contain interesting comparisons, but until fuller data are gathered no definite conclusions can be drawn.
5. The deer trapped in Alpena County were heavily infested with nosefly larvae (*Cephenomyia phobifer*) and lung worms (*Protostrongylus rufescens*), but just how serious these are has not yet been determined.
6. Deer tagged and released where they were caught during the yarding season have been reported from as far as 17 miles away the following November.
7. Adult deer transferred and released may return as far as 15 miles to the place where they were caught.
8. So far as is known, fawn deer transferred and released do not return from distances of $5\frac{1}{2}$ miles.
9. Deer transferred and released more than 20 miles from where they were caught seem to be in strange country and show

no tendency to drift in the direction of "home," but will apparently scatter in any direction from the point of release.

10. During the 1931 deer-hunting season 14.7 per cent of the bucks tagged during the previous January, February, and March were shot and reported on.

Department of Conservation
Lansing, Michigan

EGGS AND YOUNG OF THE SMOOTH GREEN SNAKE, *LIOPELTIS VERNALIS* (HARLAN) *

FRANK N. BLANCHARD

WHILE the writer was in residence at the University of Michigan Biological Station during the summers from 1924 to 1931, opportunities were taken to gather information bearing on the habits and the life-history of the smooth green snake, *Liopeltis vernalis* (Harlan). Although common in Cheboygan and Emmet counties (that part of the Lower Peninsula of Michigan just south of the Straits of Mackinac), the green snake is too generally distributed and too inconspicuous to be a profitable object for specific search. Specimens are brought in occasionally by members of the Station, and they are sometimes captured on general snake-hunting trips. In this way about five or six females with unlaid eggs have been obtained each season. Such specimens were kept in separate cages until their eggs were laid, and the eggs in turn were kept with slightly damp, rotted wood in closed containers until they hatched. Enough information has now accumulated on certain topics to warrant publication.

This work has been aided during the past two seasons by grants from the Research Fund of the University of Michigan. For this assistance the writer is very grateful. In the keeping of records Miss Ethel B. Finster of Asheville Normal School, North Carolina, has helped very materially. Aid of this nature has also been given by Carl O. Erlanson. Among the many members of the Biological Station who have contributed specimens Elmer E. Brown should be especially mentioned.

LAYING OF EGGS

Although the eggs were usually found after they had been laid, their deposition was observed on several occasions. Almost any

* Contribution from the Biological Station and the Zoölogical Laboratory of the University of Michigan.

position may be taken by the female. The one shown in Plate LI, Figure 1 is sufficiently typical. Here the sixth egg is shown distending the body just forward of the anus. The actual extrusion of an egg is depicted in Figure 2. This shows the deposition of the last egg of a set of six. From the appearance of the egg in the vent to its complete expulsion about four to six minutes elapse, but the greater part of the egg emerges too rapidly to be photographed halfway out, unless the light is sufficiently intense for an instantaneous exposure. Near the beginning of the process there is a pause while the tail is arched proximally in a sharp curve, and again at the end, just before the vent is finally lifted away from the egg, there is another pause. After the eggs are laid the body is much shrunken.

Exact intervals between the deposition of eggs of a set were recorded in ten cases. These varied from 15 to 67 minutes, with an average of 34 minutes. Although most of the sets were laid in one continuous process occupying only a few hours, there were some instances of the lapse of a day or longer between the appearance of the first one or more eggs and the remainder. Thus two eggs of the seventh set were laid in the morning of August 15, two more on the 16th, and three more early on the 18th, or during the preceding night. All but the third and seventh of these eggs hatched. In the thirty-seventh set the first egg was deposited early on July 30 and the remaining six were laid three days later. All the eggs hatched.

Sometimes, however, such an interval during the laying of a single set of eggs accompanied abnormal conditions. For example, in the twenty-first set one egg was laid early on August 13 and the second just four days later. Two days after that the parent died, with three unlaid eggs. Clearly this was not a normal case, although the first two eggs hatched (September 4 and 5).

In another instance (the twenty-fifth set) one egg was laid on July 25 and three were laid on August 1. All four hatched normally, the first two on August 12 and the last two three days later. But on July 24, the day this female was collected, there was a sunken spot in front of the anus large enough to make it appear that an egg had just been laid. The shock to the snake

from the collecting may, in this case, have been responsible for the irregular deposition of the eggs.

In thirty-four cases there were only four in which any considerable time intervened between the appearance of the first eggs and any subsequent ones of the same set.

Several times it has been observed that rough handling of the female causes premature deposition of the eggs. This sometimes happens when an inexperienced person collects the snake. Such eggs have not hatched.

After the eggs are laid the parent may remain coiled about them for several hours, if not disturbed, but after she has once left them she does not return to them nor show any interest whatever in them.

DESCRIPTION OF EGGS

As the egg appears in the vent of the female, and just after its deposition, it is moist and translucent (Pl. LI, Fig. 2). If in this condition it touches any egg previously laid, it adheres to it when it dries. Thus, whether all the eggs of a complement are stuck together in a cluster or are more or less separate depends upon the movements of the female during oviposition and the chance contacts of the eggs as laid. A few moments after an egg is laid it becomes white and opaque all over. If kept in perfectly clean surroundings, it retains this pure, white appearance until hatching, but contact with damp substances discolors it (Pl. LI, Fig. 1).

The eggs are, as a rule, cylindrical, with blunt-rounded ends, but sometimes one end is more pointed than the other (Pl. LI, Fig. 3; Pl. LII, Figs. 4 5). The covering shell, or membrane, is unusually thin for a reptilian egg.

The eggs vary in length from 19.5 to 34.0 millimeters and in diameter from 8 to nearly 18 millimeters. However, of those measured the great majority fall within the limits of 20 to 30 by 10 to 15 millimeters. The longest eggs have never had also the greatest widths (Fig. 51). The type of variation in size and shape within a single set is shown in Figures 3–5 of Plates LI and LII.

In a day or two after being laid the egg becomes plump and the shell smooth and taut. Measurements show a slight increase in length and width, but there is no noticeable change in shape.

Some eggs never become plump and may even become considerably shrunken, but the young snakes may be expected to hatch normally from even very unpromising-looking eggs.

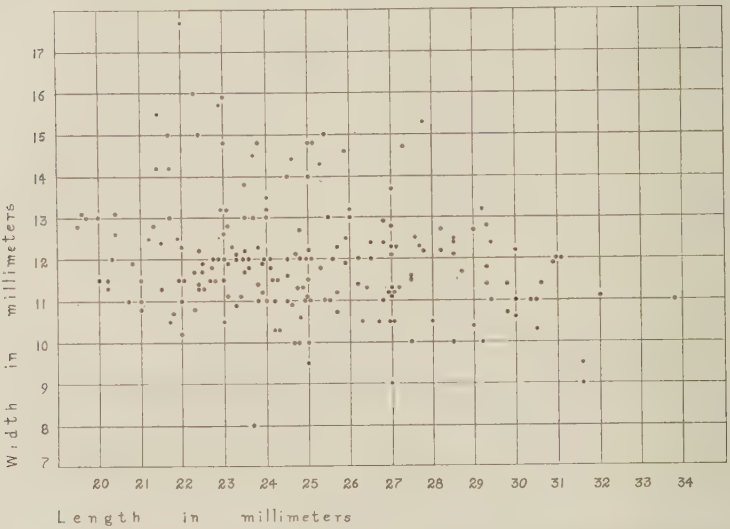


FIG. 51. Dimensions of eggs of green snake, measured when freshly laid or as discovered in natural nests. Each dot represents one egg

DATES OF LAYING EGGS

The fact that the green snake lays its eggs late in the summer was recognized by Surface as early as 1906 (p. 165), when he stated that "the laying may occur from the 12th of August to the 15th of September." He mentioned no specific instances, however. Although the dates of egg-laying must vary with the season and the locality, still there has been no subsequent verification of Surface's statement that eggs are laid in September, except for a doubtful record published by Bishop in 1927 (p. 79). Here the statement is made that "a specimen taken August 21, 1926, deposited two eggs then and four more on Sept. 2. Deposition of the first two was probably due to rough handling." The last

statement is probably correct, but when part of the process is premature there is at least the possibility that the remainder is not normal.

Records for deposition of eggs obtained from captive females by the writer cover the period from July 24 to August 29 (Fig. 52). All other records that are known to him, including those of the discovery of eggs in the field, fall within this period. Professor Frank Smith has informed him of a set of seven eggs laid in the laboratory at Douglas Lake on August 8, 1920; Bishop reports eggs found at Allegany State Park on August 11, 1922, and August 12, 1923 (1927, p. 79); and Loveridge found eggs near Boston, Massachusetts, on July 28, 1925 (1927, p. 55).

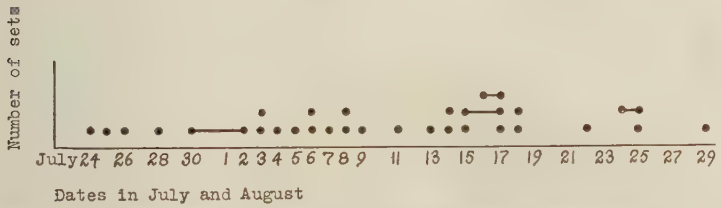


Fig. 52. Dates of laying of eggs of *Liopeltis vernalis* in laboratory at University of Michigan. Circles joined by lines indicate sets requiring more than one day for their deposition

In addition, the writer found eight sets of unhatched eggs in the field in northern Michigan on July 31 and August 5, 1930, and July 29, 1931. Females with unlaid eggs have been found all through July and on August 2, 6, 7, 8, and 12 in different years. An early date for laying is indicated by a specimen found July 20, 1930, with abdomen shrunken exactly as if it had laid eggs on that day. In this connection it is worth noting that the earliest dates recorded, July 24 and 25, are in this same year, a season that proved exceptionally early for other biological events.

The data at hand all indicate, therefore, late summer as the egg-laying season for the smooth green snake — more specifically, in northern Michigan the eggs are usually laid during the first three weeks of August, although they should be expected for a week or more earlier and later than this.

NUMBER OF EGGS IN A COMPLEMENT

The number of eggs in a set varied from 3 to 11 in the 41 clutches studied. The commoner numbers were 4 to 8, the commonest 7. Several additional records have come to hand from various sources. In the summer of 1922 a specimen of *Liopeltis* at the Biological Station of the University of Michigan laid seven eggs. Professor Frank Smith has informed the writer of a female that laid seven eggs in a vivarium on August 8, 1920; and of another, collected on July 8, 1920, that was found, on the following day, after it had died, to be a female with eight eggs. Professor Max M. Ellis reported a set of six eggs at the same place in 1914 (1917, p. 49). A set of nine eggs is reported by Fisher (1921, p. 23); sets of three and four are recorded by Langlois (1924, p. 607); a set of ten is mentioned by Loveridge; and two clutches of six and one of seven are mentioned by Bishop (1927, p. 80). Dissections by the writer have given the following complements: 4, 6, 7, 7; and nests of empty shells have furnished the numbers 5, 5, 6, and 11.

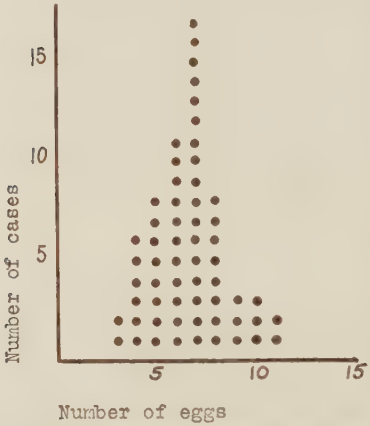


FIG. 53. Diagram showing the number of eggs in a full set. Records previously published as well as new ones are included

All these records of the number of eggs in a set are summarized in Figure 53.

DATES OF HATCHING OF EGGS

Dates of hatching of forty-one sets of eggs covering the years from 1924 through 1931 have varied from August 5 to September 4 (Fig. 54). Further records may extend this period somewhat at each end. It is unlikely, however, that the hatching period in

any one season is as long as this, for the longest noted in a single summer (1930) was seventeen days.

Published records of hatching under laboratory conditions fall within the dates given above. Ditmars (1907, p. 326) found a set of eggs in Sullivan County, New York, on August 14 that hatched on the 25th of that month; Ellis (1917, p. 49) found six eggs at Douglas Lake on August 18, 1914, that hatched on August 20; Langlois (1924, p. 607) recorded two sets, totaling six eggs, all of which hatched August 28, 1923; and Loveridge

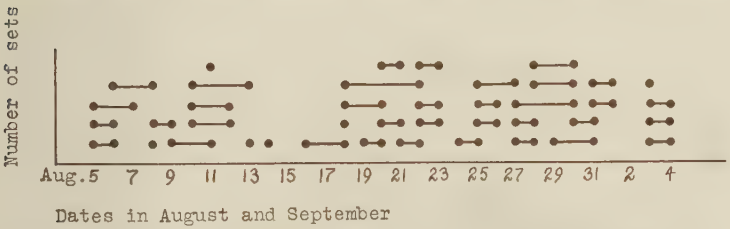


FIG. 54. Dates of hatching of sets of eggs under laboratory conditions. A single circle indicates that all the eggs of a set hatched on the same day; two circles joined by a line indicate that two or more days were required for the hatching of the whole set

(1927, p. 55) had a set of ten eggs that hatched from August 20 to 23, 1925.

There are a few records for the hatching of eggs under natural conditions. Fisher (1921, p. 23) visited a set of eggs in Oxford County, Maine, every day for a week until hatching began on August 30, 1920. On August 5, 1930, a set of seven was found at Big Stone Bay, of which one egg was hatched when discovered, two were hatching and the young snakes came out immediately, another hatched before our return to the laboratory, two more cracked that evening, and the last egg hatched the next day. Of another nest of eleven eggs found on August 5, 1930, one egg was cracked when examined on return to the laboratory, and the remainder hatched in the next two days. Of a third nest found on the same date, one egg had hatched, one was just hatching, three were cracked, and emergence of all the young snakes took place within the next two days. On August 13, 1931, three clusters of

recently hatched green snake eggs were found in close proximity. One group contained eleven dry shells, another five collapsed shells still moist, and the third five collapsed shells so moist that the young snakes must have left within a day. In another locality, on August 14, 1931, a young green snake was found only 137 millimeters in length. It was not more than a few days old, since it had not yet shed its skin. Thus the dates of hatching under natural conditions match the dates obtained in the laboratory.

LENGTH OF PERIOD FROM LAYING TO HATCHING

The time elapsing between the laying of the eggs and their hatching varied in the cases under observation from four to twenty-three days. The variation within one set of eggs is, however, commonly a little less than two days, although in one case it was three and in others all the eggs of a set hatched in the same number of days.

The only published record for the interval between laying and hatching is that of Langlois (1925, p. 607), who mentions two sets that hatched in fourteen days.

A summary of the number of days of development from laying to hatching for all eggs that completed apparently normal development is presented in Figure 55. Reduction of this interval to four days in some cases suggests the possibility of occasional ovoviviparity in this species.

HATCHING

The actual process of hatching is a rather long and interesting one. Some of the details were noted by Fisher (1921), who found eggs hatching in the field, but it remained for Langlois (1925) to describe the process more fully. Two years later Loveridge detailed the hatching of a set of eggs under laboratory conditions. These accounts are, however, so brief as to make desirable a presentation of the subject in greater detail.

The movements of the young snake within the egg eventually become too much for the thin, membranous shell, and a slit appears nearly or quite lengthwise of the egg somewhere on the upper side. This is doubtless caused by the egg tooth, which is plainly

visible when the head is protruded from the egg. At the first slit in the shell a large drop of clear liquid oozes out (Pl. LIII, Fig. 6, egg No. 1), and sooner or later the tip of a snout appears in the opening (Fig. 7). It is soon pushed out far enough to expose one eye. The young snake is now sensitive to movements and is likely to withdraw suddenly if one makes a motion toward him. The little snake may remain for several hours in this position, or with the head thrust a little farther out, but he may withdraw

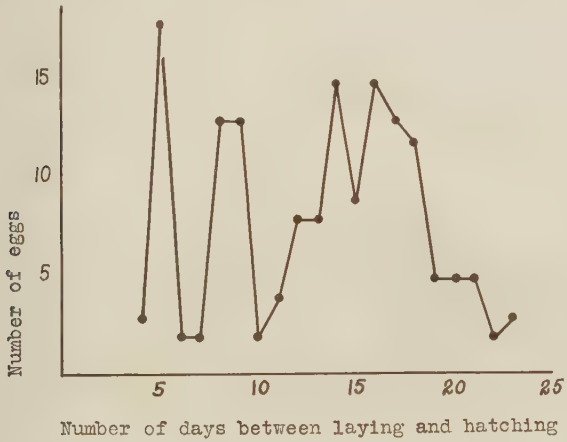


Fig. 55. Diagram showing number of days intervening between laying and hatching of eggs of *Liopeltis vernalis*

within the shell and thrust his head out again, sometimes in a new place. If the egg is turned upside down the young snake will promptly orient himself and break through a new opening in the upper side.

After a few hours he becomes more restless, his movements are more frequent, and his head is put in and out many times, during which several more slits are likely to be made in the shell. The head is eventually thrust out farther, and even a third or more of the body may be extended. The snake may leave the shell at any time now. He emerges slowly and directly until wholly free. He is wet all over and particles of dirt stick to his

body, but after moving about in exploration for about five minutes he is clean and dry. Final emergence normally takes only about two minutes, and in a few minutes more the young snake is dry and fully active. Various steps in the hatching process are illustrated in Plates LIII to LVI.

The interval elapsing between the first cracking of the egg and the complete emergence of the young snake — the emergence interval – has been timed by numbering the eggs and keeping close watch of them. Sixty-two have been timed to within a small fraction of an hour and seven more to within one hour. These vary from $1\frac{1}{2}$ to $40\frac{1}{4}$ hours, but 80 per cent of them vary from only 14 to 28 hours (Fig. 56). In brief, most young snakes leave the

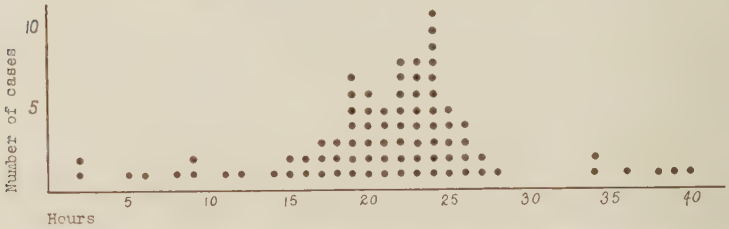


Fig. 56. Diagram showing number of hours from first cracking of shell to complete emergence of young snake

egg about 24 hours, or a little less, after the first slit appears in the shell. Out of fifty-eight in which the emergence interval was not determined exactly, only one was recorded in which it was greater than the maximum given above, i.e. between 55 and 60 hours.

The snakes that emerge in the shortest intervals recorded are likely to be premature. They are not free from the yolk stalk and are obliged to wait and struggle for many minutes, or even hours, before finally pulling free.

The interval from the emergence of the first snake of a clutch to the emergence of the last one usually varies from a little more than one day to a little less than two days, although two days or a little more is not uncommon, and there is one record of three days. From the first crack of an egg to the last emergence in that

clutch about one day longer is required. This interval, which may be considered the hatching period, may then be stated as about two to three days.

As a rule, the eggs probably hatch in the same order in which they are laid, although for only three sets of eggs are the data reasonably complete. This information is summarized in Table I. It will be observed that four of the eggs of Set 7 conform to this rule, but eggs numbered 4 and 7 hatched earlier than some laid earlier. This applies also to the cracking of the eggs. Of Set 24 the first four eggs conform to the rule, but the fifth does not. The latter egg was also unusual in having a very short emergence interval. In Set 28, for which the data are complete in every respect, slitting and hatching of the eggs follow exactly the order of laying.

Since the eggs form a single line in the body of the snake during their period of development, the most posterior, which are laid first and which ordinarily hatch first, must have been fertilized first. Therefore, since hatching follows closely the order of fertilization, the period of gestation or development must in itself be very definite, even though subject to variation from numerous causes. It is probable, then, that the eggs are ordinarily shed from the ovaries to the oviducts as one process, which takes about as long as the laying or the hatching.

The interval from copulation to hatching is not the gestation period, for as numerous dissections on other species of snakes, in particular *Thamnophis sirtalis*, have shown, copulation takes place while the eggs are very small and presumably furnishes the stimulus for their growth. After copulation the spermatozoa slowly make their way forward until they reach the anterior portions of the oviducts. Here they wait several weeks, perhaps a month or more, for the eggs, and here the eggs are fertilized. The gestation period begins, of course, at this time.

THE YOUNG SNAKE

The length of the young snake on emergence from the egg most commonly lies between 114 and 131 millimeters, but extreme variants from 101 to 166 millimeters have been noted. The

TABLE I

Showing Relation between Time of Laying and Time of Hatching of Eggs of *Liopeltis vernalis*

Set No.	Egg No.	Laying of eggs		Cracking of eggs		Emergence of young		Emergence interval in hours
		Date	Hour	Date	Hour	Date	Hour	
7	1	Aug. 15, 1925	10:00–12:00 A.M.	Aug. 27	4:45 P.M.	Aug. 29	9:00 A.M.	40¼
	2	Aug. 15, 1925	10:00–12:00 A.M.	Aug. 28	10:25 A.M.	Aug. 29	10:45 A.M.	24⅓
	3	Aug. 16, 1925		Spoiled				
	4	Aug. 16, 1925		Aug. 27	8:45 A.M.	Aug. 28	9:15 A.M.	24½
	5	Aug. 17–18, 1925	5:00 P.M.–9:00 A.M.	Aug. 28	8:45 P.M.	Aug. 30	7:00 A.M.	34
	6	Aug. 17–18, 1925	5:00 P.M.–9:00 A.M.	Aug. 29	9:25 A.M.	Aug. 30	8:15 A.M.	22½
	7	Aug. 17–18, 1925	5:00 P.M.–9:00 A.M.	Aug. 28	10:50 A.M.	Aug. 29	9:12 A.M.	22⅓
24	1	July 25, 1930	?	Aug. 8	10:30 A.M.–6:30 P.M.	Aug. 9	11:15 A.M.	Between 17 and 25
	2	do.	7:17 P.M.	Aug. 8	10:30 A.M.–6:30 P.M.	Aug. 10	8:30 A.M.	Between 38 and 46
	3	do.	7:36 P.M.	Aug. 9	1:00 P.M.–3:00 P.M.	Aug. 10	9:30 A.M.	Between 18½ and 20½
	4	do.	8:01 P.M.	Aug. 9–10	8:30 P.M.–7:30 A.M.	Aug. 11	1:30 P.M.	Between 30 and 41
	5	do.	8:35 P.M.	Aug. 9	9:00 A.M.	Aug. 9	10:45 A.M.	1¾
28	1	Aug. 4, 1930	7:51 P.M.	Aug. 21	8:00 A.M.	Aug. 22	10:00 A.M.	26
	2	do.	8:26 P.M.	Aug. 22	11:00 A.M.	Aug. 23	8:30 A.M.	21½
	3	do.	9:05 P.M.	Aug. 22	12:30 P.M.	Aug. 23	10:00 A.M.	21½
	4	do.	9:34 P.M.	Aug. 22	3:00 P.M.	Aug. 23	3:00 P.M.	24

length of the snake may be correlated to some extent with the size of the egg, but evidence of it is not clear, nor does there appear to be any relation between length and sex.

The lengths, as determined by gently straightening the young snakes along a ruled edge, are shown diagrammatically in Figure 57.

The color of the newly hatched snake has but slight suggestion of green. In general terms it may be described as a somewhat shiny, dark olive-gray above, becoming lighter on the sides; the first row of scales, and often a part of the second, are distinctly lighter than the rest; the sides of the head are greenish, the lower parts pale grayish blue. By comparison with Ridgway's *Color Standards*, the upper side is generally dark olive-gray, some-

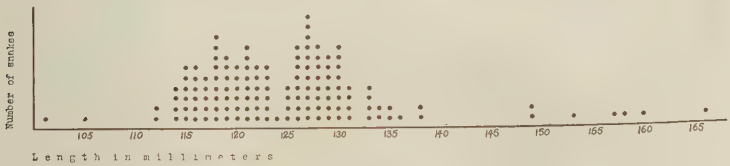


Fig. 57. Diagram showing lengths of green snakes at birth

times deep mouse-gray, less often deep neutral gray, dusky green-gray, iron-gray, or dark olive-gray to iron-gray; the lower surfaces are pale Medici blue or glaucous gray.

The interval between hatching and first shedding of the skin seems to vary considerably. Although the commonest interval recorded was six days, it has been noted as short as one day and as long as seventeen. The amount of moisture in the environment may be an important influence.

After shedding, the young snake is distinctly green above — a velvety olive-green — and white below, with the first row of scales and sometimes part of the second of a buff color. By comparison with Ridgway's *Color Standards* the young snake is now olive-green, yellowish olive, Lincoln green, or dark greenish olive above, becoming greener on the head and lighter on the sides; the first row of scales, or a little more, is pale yellow-orange or cream-colored; the lower surface is almost white.

Young snakes after shedding are much like adults in appearance, in disposition, and in habits. That they are rarely encountered by collectors must be due to their small size, inconspicuous color, and lack of tendency to seek shelter in such places as collectors investigate.

They feed readily on small spiders when they can catch them, and on various kinds of insects. Ant pupae were picked up and swallowed after more or less sensing with the tongue. One individual ate two small, smooth, green lepidopterous larvae and refused a third. Another ate a small grub when it was put in front of him. It had lain in the cage untouched, however, for several days. One snake took a pentatomid bug, when it was offered, as readily as if it had been a spider. When the bug was about three fourths in the snake's mouth, it was suddenly ejected with evident signs of dislike on the part of the snake. Little snakes showed much interest in a small black cricket and followed it, but the cricket was too active to be caught. They showed no interest in a sow bug, centipede, earthworm, slugs, and ants.

SUMMARY

1. The eggs in a set of the smooth green snake are ordinarily laid as one continuous process. The intervals between successive eggs vary from fifteen minutes to an hour or more, though in a few instances a day or longer has elapsed between the appearance of the first eggs and the remainder. In some of the latter cases, however, it is evident that the conditions were not normal.

2. The parent shows no interest in her eggs.

3. The eggs are generally cylindrical, with blunt-rounded ends. The shell, or membrane, is white and opaque, and unusually thin for a reptilian egg.

4. The eggs vary in length from 19.5 to 34.0 millimeters and in diameter from 8 to nearly 18 millimeters. Most commonly, however, they vary within the limits of 20 to 30 and 10 to 15 millimeters.

5. The number of eggs in a clutch has varied in the cases observed, and in those reported to date, from 3 to 11. Seven is the commonest number.

6. Eggs are usually laid during the first three weeks of August, although they may be deposited a week earlier or later than this. Extreme dates on record are July 24 and August 29.

7. The hatching period in northern Michigan varies from August 5 to September 4, and these dates include all the records from other localities. In any one year the longest hatching period has proved to be only seventeen days.

8. The interval from laying to hatching varied in the cases under observation from four to twenty-three days. Among the eggs of the same complement the variation in this interval is commonly a little less than two days. In some sets all the eggs hatch in the same number of days; in others the variation may be as much as three days. The possibility of occasional ovoviviparity in this species is suggested by this very brief interval.

9. Hatching is a process ordinarily requiring many hours, during which the snout or head of the young snake appears and disappears many times through the slit in the egg shell. This period commonly varies from fourteen to twenty-eight hours. A period of two to three days is generally required for all the eggs of a clutch to complete the hatching process.

10. The order of hatching of the eggs of a set conforms approximately to the order in which they were laid.

11. Newly hatched snakes vary, commonly, from 114 to 131 millimeters in length, although extremes of 101 and 166 millimeters have been noted. They are dark olive-gray above, lighter on the sides, and pale grayish blue below. After the first shedding of the skin, which takes place in a few days, the color above is a velvety, olive-green, and the underparts are white.

12. The feeding habits of the young snakes are similar to those of the adults. Individuals were observed to eat spiders, ant pupae, smooth, green lepidopterous larvae and grubs, and to refuse a pentatomid bug, ants, slugs, centipedes, earthworms, and sow bugs.

University of Michigan

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FIG. 1. Green snake about to deposit an egg

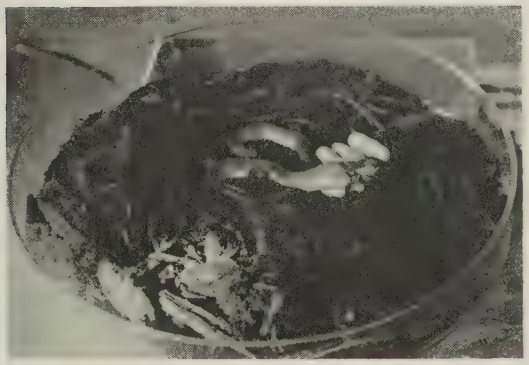

FIG. 2. Green snake laying an egg, which is not wholly free from the anus

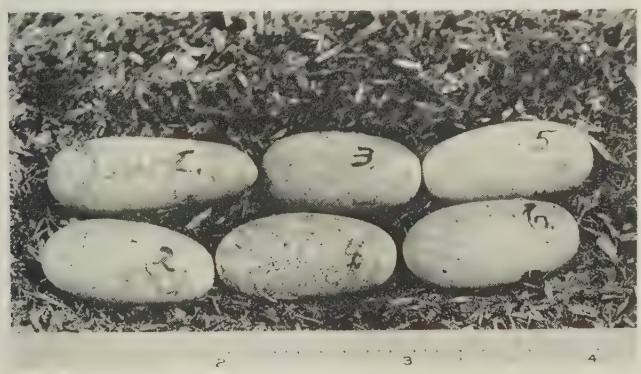

FIG. 3. Set of six eggs of green snake

PLATE LII

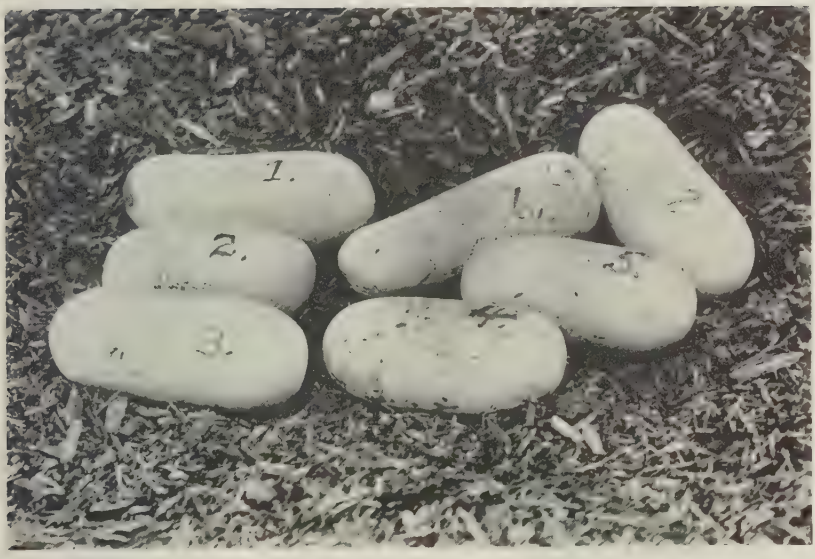

FIG. 4. Set of seven eggs of green snake

FIG. 5. Set of six eggs of green snake

Fig. 6. Hatching of the eggs of Set 7. Egg 1 has just cracked, and a large drop of clear liquid has flowed out. Egg 4 cracked a little earlier

Fig. 7. Hatching of the eggs of Set 7. The fore part of a head protrudes from egg 1. Egg 4 is represented by a collapsed shell; the snake has escaped

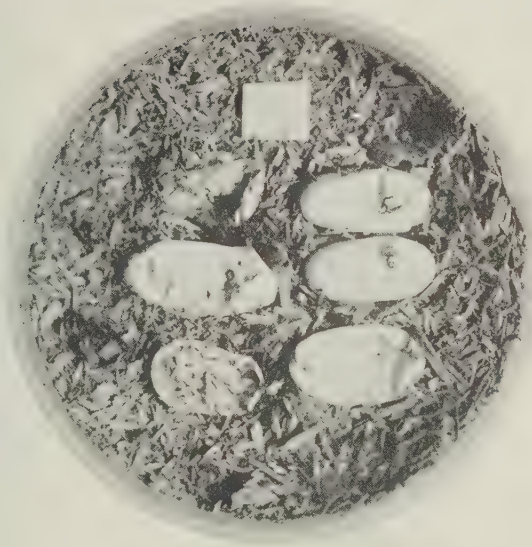

FIG. 8. Hatching of the eggs of Set 7. Eggs 1, 4, and 7 have hatched; a snout protrudes from eggs 5 and 6, and nearly a whole head appears from the upper right-hand portion of the second egg

FIG. 9. Hatching of the eggs of Set 8. Three eggs are not yet cracked. Two collapsed shells show that snakes have emerged, and a young snake lies near the center of the figure. Evidently it has very recently emerged, for particles of rotted wood adhere to its body

FIG. 10. Hatching of the eggs of Set 8. Only one egg remains uncracked; a head protrudes from each of the two eggs in the center, and a recently hatched snake lies coiled at the left

FIG. 11. Egg of green snake in process of hatching

FIG. 12. Another egg in process of hatching

REPORT ON NUISANCE-BEAVER CONTROL, 1931

GLENN W. BRADT

THE Conservation Commission, in April, 1931, authorized the employment of special crews for beaver control, whose duty it should be to live-trap beavers in places where they were doing damage, and to transfer them to other places where they would be desirable and could be given adequate protection. This action was taken in response to the increasing number of complaints by landowners and others that beavers were plugging culverts, flooding roads, railroads, and pasture lands, and cutting valuable trees. A complaint form was to be signed by complainants, after which the alleged damage was to be investigated by the local conservation officer, upon whose recommendation the control crew would start operations. The first live-trapping operations, except for a few sporadic efforts by local conservation officers, were undertaken by G. W. Bradt of Michigan State College, assisted by officers Deuell and Fike, on the Jordan River in Antrim County, on April 25. On April 27 Mr. L. A. McIntire of Boyne City, who had already done some live-trapping for beaver breeders, was secured to carry on the work. Mr. Bradt was obliged to return to the college on May 2, having been on temporary leave to secure live, pregnant, female beavers for the experiment being carried on there. Mr. McIntire continued to trap beaver most of the time until October 8; he was assisted in the Upper Peninsula from July 13 to September 23 by A. M. Stebler. Edward Wood and Joseph Artibee were employed in the Upper Peninsula from June 8 to July 13, and again from August 1 to August 17.

G. W. Bradt was employed from June 20 to September 1, working with McIntire and Stebler in the Lower Peninsula from June 20 to July 14; with Artibee from July 14 to July 30; alone from August 1 to August 17; and again with Artibee from August 17

to September 1. Artibee continued the work alone much of the time from September 1 to November 7. Live-trapping was carried on by means of the Bailey type of live-trap and the new type of aluminum trap. The latter type gave the best service, and is probably the most satisfactory live-trap obtainable at the present time.

Live-trapping was carried on in seven counties in the Lower Peninsula and in twelve of the Upper Peninsula.

The tables on the opposite page show the results of live-trapping in the state in 1931.

The large number of beavers listed as adults (unsexed) is due to the fact that determination of sex is very difficult. The sex organs are entirely internal, with no external sex characteristics except in a female which is suckling young. Hence much skill and practice are necessary to sex the animals, and also suitable apparatus for holding them in a safe position for examination. The beavers caught by Artibee and by Artibee and Wood were unsexed. Many of those caught by McIntire were unsexed also, since sexing is very difficult for a man to accomplish without assistance.

By the term "case" in the tables is meant the operation of removing beavers from the scene of a complaint. Those locations which upon inspection proved to be without beavers or in which the complaints were found to be unjustified, are not counted in the tables.

The average number of beavers caught per case in the Lower Peninsula was 3.2; in the Upper Peninsula, 3.5. The average number of days spent in trapping per case in the Upper Peninsula was 6.0; in the Lower Peninsula, 6.6. These averages, though accurate so far as each individual case is concerned, do not indicate the actual time spent in disposing of a case. Quite often more than one case was handled at the same time. Sometimes as many as three or four were taken care of at once. Therefore, the average time as stated above is the average necessary in order to be sure that the beavers are all removed at a particular place, but usually more than one case can be handled at the same time.

During the entire season but sixteen beavers were lost by death

TABLE I

Upper Peninsula

County	Adult males	Adult females	Kits	Adults (unsexed)	Total	Cases
Alger	0	1	5	4	10	6
Chippewa	5	3	12	2	22	5
Delta	0	0	0	2	2	1
Dickinson	4	3	2	6	15	3
Houghton	2	1	5	0	8	2
Iron	6	2	11	5	24	7
Keweenaw	3	1	3	0	7	3
Luce	1	1	2	2	6	3
Mackinac	0	0	0	2	2	2
Marquette	13	24	11	33	81	23
Menominee	0	0	0	2	2	1
Schoolcraft	1	0	0	4	5	2
Totals	35	36	51	62	184	58

TABLE II

Lower Peninsula

County	Adult males	Adult females	Kits	Adults (unsexed)	Total	Cases
Antrim	2	0	0	11	13	3
Charlevoix	3	0	0	19	22	5
Cheboygan	0	3	7	18	28	7
Gladwin	1	1	0	0	2	1
Montmorency	1	1	0	2	4	2
Otsego	0	0	0	2	2	3
Presque Isle	1	9	4	1	15	4
Totals	8	14	11	53	86	25

TABLE III

Results for the Entire State (Tables I and II Combined)

Adult males	Adult females	Kits	Adults (unsexed)	Total	Cases
43	50	62	115	270	83

in live-traps. Since two hundred and seventy beavers were captured, this represents a loss of only 6 per cent. All the beavers were found drowned in the traps. Some of these deaths were due to the trap's slipping into deep water and thus submerging the beavers. Nearly all such fatalities could be prevented by properly fastening the trap after setting. Some of the deaths were apparently due to the beavers' permitting themselves to sink below the water surface and drown, after getting chilled in traps and weakening, although traps were not entirely submerged. There seems to be considerable individual variation among beavers in ability to withstand exposure. The aluminum traps close with a powerful snap; they are shorter than the older models, and might be expected to catch large beavers between the edges of the jaws occasionally, but in no instance was there any evidence that a beaver had been injured by a trap.

Every beaver killed was skinned, and the skin was sent to the Lansing office of the Conservation Department. It is a wise requirement that every dead beaver must be skinned and the skin turned in, since skinning in warm weather is disagreeable work and the trapper will be very careful to avoid losing animals through either careless setting of traps or careless handling after capture, if he is obliged to skin every dead animal.

Almost all the beavers taken during the summer were tagged on the tail; the tags are stamped with the words "Conservation Department" and with the individual tag number. Unfortunately, evidence has been accumulated which indicates that these tags work out of the tail within a year or two after tagging, which makes their use of doubtful value. A method of branding numbers on the tails is now being developed. At present branding seems to be successful, but it will be necessary to wait at least two years before success or failure can be definitely announced. There is no difficulty about handling the beavers to brand or tag them. Neither operation seems to hurt them. An occasional beaver will flinch when the tag is punched through the tail, but most of them do not appear to feel the punch at all. Branding with a hot iron creates a lot of smoke and odor, but the animals themselves never give the least evidence of pain during the operation.

The total expense of beaver control for 1931 was $4,639.16. This makes the average expense per beaver for the season $17.18, about the value of a good prime beaver pelt. These beavers were liberated in places where their presence is considered desirable by the Conservation Department, and certainly the cost per beaver was not an excessive amount, since it is not probable that live animals in good condition could have been secured at so low a figure from any other source.

Michigan State College
East Lansing, Michigan

NOTES AND STUDIES ON ARACHNIDA. IV

ARANEAE FROM THE DOUGLAS LAKE REGION, MICHIGAN. II *

ARTHUR M. CHICKERING

FROM August 7 to August 17, 1931, the author of this brief paper collected Araneae for the second successive season in the vicinity of Douglas Lake, Michigan, the site of the Biological Station of the University of Michigan. From this second collection fifty-five species have been identified, thus bringing the total number definitely known from this part of the state to one hundred and twenty-six. Though the list of identified species is not large as compared with the lists from a few parts of the country where collections have been made more or less continuously for many years, nevertheless a substantial beginning has been made. The intention is steadily to continue this work until we know quite accurately the extent of this portion of the fauna of Michigan. It will be greatly appreciated if biologists working at the Biological Station of the University of Michigan will coöperate with me by sending me any Arachnida, especially Araneae, which may come into their possession in the course of their own collecting activities. The method of preserving these animals in 95 per cent alcohol is so simple that little time will be lost by those who desire to coöperate.

SUB-ORDER ARACHNOMORPHAE

AGELENIDAE

On the basis of Chamberlin's recent work (1925) on spiders ordinarily assigned to the genus Coelotes, I have listed as follows the three species now included in my collection from the Douglas Lake region:

* A contribution from the biological laboratories of Albion College and the Biological Station of the University of Michigan.

Coras montanus (Emerton). — There can be little doubt that this species is the one originally described by Emerton as *Coelotes montanus*. It appears to be fairly common. Known from Ontario, Newfoundland, Connecticut, New York, and the region of Lake Superior.

Coras juvenilis (Keyserling). — This is the species listed from my collection of 1930 as *Coelotes fidelis*. Reported from New England to Nebraska. One mature female, with perhaps several immature individuals.

Wadotes calcaratus (Keyserling). — This is the species formerly identified as *Coelotes calcaratus;* it is known from Maine, New Hampshire, Massachusetts, Connecticut, Maryland, Washington, D. C., North Carolina, New York, Indiana, Illinois, Nebraska, and Kentucky. Appears to be quite common in Michigan.

PISAURIDAE

Dolomedes triton sexpunctatus Hentz. — Spiders of this species have been taken during both seasons of collecting at Douglas Lake and appear to be common. This species was listed in 1931 as *D. triton,* but is regarded as the northern form of this species, formerly known as *D. sexpunctatus,* by Bishop (1924).

Dolomedes sp. (?). — I have four immature specimens which clearly belong to another species of this genus, but they have not been definitely placed.

LYCOSIDAE

Alopecosa beanii Emerton. — This species was described from Canada and has since been found in Maine and New York. I seem to have taken one female at Douglas Lake.

Lycosa fatifera Hentz.

Lycosa helluo Walckenaer.

Lycosa pikei Marx.

Lycosa pratensis Emerton.

Lycosa sp. (?). — Several specimens of a large Lycosa from Sturgeon Bay beach, where it makes burrows without turrets.

Pardosa saxatilis (Hentz).

Pirata insularis Emerton.

Pirata minutus Emerton. — A very common species in this region. I have found many in the bogs among sphagnum plants. Also the smallest species occurring here. Best known hitherto from southern New England and New York.

Pirata montanus Emerton.

DICTYNIDAE

Dictyna foliacea (Hentz). — The dictynas appear to be a very common genus among the small herbaceous plants, where they build webs in the flower heads and among the leaves. This species is known from Ottawa, from New England to Florida, and westward to Utah and Washington.

Dictyna volucripes Keyserling. — Also widely distributed from Massachusetts to North Carolina, and to Colorado and Utah.

THERIDIIDAE

Argyrodes trigonum (Hentz). — One female not quite mature, about 2.5 mm. in length. This interesting spider is distributed from the northern United States through Mexico and Central America to northern South America. It is believed to live as a commensal with several of the larger species.

Crustulina guttata (Wider). — A European species, common in the eastern states. Now occurs westward as far as Nebraska.

Latrodectus mactans (Fabricius). — This species is distributed from southern Canada southward over most of the United States through Central America and South America. Only one immature female has thus far been collected in Michigan.

Theridula opulenta (Walckenaer). — This is a cosmopolitan species of nearly all latitudes and is highly variable.

LINYPHIIDAE

Ceraticelus fissiceps (Cambridge). — Two males of this species measuring about 1.5 mm. each. Well known in New England and New York. It extends southward as far as North Carolina and westward as far as Nebraska, according to Worley and Pickwell (1931).

Drapetisca alteranda Chamberlin. — This is the only species in this genus occurring in this country. It is believed to spin no web. Well known in New England and New York. Probably common in Michigan and surrounding states.

Linyphia clathrata Sundevall.

Linyphia insignis Blackwall. — A European species now well established in this country and known from New England, New York, New Jersey, Pennsylvania, and now Michigan.

Linyphia lineata (Linnaeus). — Also a European species; more widely distributed in America than the former species.

Linyphia variabilis Banks. — Described from New York and apparently not very common.

Tapinopa bilineata Banks. — Well known from the eastern states from Maine to the District of Columbia.

ARGIOPIDAE

Araneus angulatus Clerck. — Widely distributed in Europe, Canada, and the United States.

Araneus nordmanni (Thorell). — Known from eastern Canada and the northeastern states.

Araneus pegnia (Walckenaer). — The open bog lands seem to be favorite places for this spider to make its silken tent and web among the low shrubs. It is regarded as occurring in all states, but was not found by Worley and Pickwell (1931) in Nebraska.

Araneus trifolium (Hentz).

Argiope aurantia Lucas. — A widely distributed species from all states, Mexico, and much of Central America.

Larinia sp. (?)

Mangora gibberosa (Hentz). — A widely distributed species over most of the United States.

Neoscona benjamina Walckenaer.

DRASSIDAE

Gnaphosa brumalis Thorell. — A northern form extending through much of Canada and the northern United States.

Zelotes depressus (Emerton). — Formerly known from Massachusetts, New York, New Jersey, and Florida.

THOMISIDAE

Oxyptila americana Banks. — Two females. Hitherto known only from New York, but listed from only one locality in that state by Crosby (1928). Probably not common.

Philodromus minutus Banks. — The tentative identification is entered here because of the finding of an egg sac believed to belong to this species.

Xysticus limbatus Keyserling. — Widely distributed over the entire United States.

Mr. W. J. Gertsch of the University of Minnesota, who is revising the genus *Xysticus*, has very kindly identified *Oxyptila americana* and *Xysticus limbatus* listed above.

CLUBIONIDAE

Castaneira descripta (Hentz). — A widely distributed species from all states.

Castaneira longipalpus (Hentz). — With about the same distribution as the preceding species.

Clubiona emertoni Petrunkevitch. — Hitherto known from New York and New England.

Clubiona pallens Hentz. — Known from Massachusetts to Alabama and westward to Nebraska.

Phrurolithus pugnatus Emerton. — Probably occurs throughout the United States, but not found by Worley and Pickwell (1931) in Nebraska.

ATTIDAE

During my collecting at Douglas Lake in 1930, mature Attidae seemed to be rather scarce. In 1931, however, the opposite condition was observed. As a result I am able to list nine additional species. A few remain unplaced. Thus eleven species now have been identified from this region. This is in contrast with fifty-seven species listed by Crosby (1928) from New York.

Evarcha hoyi (Peckham). — Well known in New England and New York. Also recorded from Ottawa and from Brazil (Petrunkevitch, 1911).

Habrocestum pulex (Hentz).

Icius formicarius Emerton.

Pellenes borealis Banks.

Paraphidippus marginatus (Walckenaer).

Phidippus purpuratus Keyserling. — Probably occurs over the entire eastern three fourths of the United States from Utah and Nebraska.

Phidippus whitmanii Peckham.

Sitticus palustris Peckham.

Tutelina elegans (Hentz).

Albion College
Albion, Michigan

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NOTES AND STUDIES ON ARACHNIDA. V

ADDITIONS TO THE LIST OF ARANEAE FROM MICHIGAN

ARTHUR M. CHICKERING AND GERTRUDE BACORN

FOR the past four years the senior author of this paper has been collecting spiders in Michigan. Intensive collecting has been carried out in only one locality in the state, the Douglas Lake region, and in it during only two short periods in the summers of 1930 and 1931. As a result of more or less desultory collecting in the southern part of the state, chiefly in the vicinity of Albion, a considerable number of spiders have accumulated since the spring of 1928. Small collections have been donated by Drs. Paul S. Welch and Peter Okkelberg of the University of Michigan, to whom our thanks for their coöperation are gratefully extended.

In the summer of 1931 the junior author began the work of carefully studying these collections from the southern part of the state under the direction of the senior author. Although the work is far from complete, nevertheless we have at least superficially examined the whole collection. Many species, of course, are the same as the senior author has already listed from Douglas Lake (Chickering, 1932, 1933). Those not hitherto reported from the state and collected elsewhere than in the vicinity of Douglas Lake number forty-nine species and constitute our third list from Michigan. From the Southern Peninsula we now have definitely listed about one hundred and seventy-five species. It is expected that an extended period of field work will be carried out during the present summer (1932) in the Northern Peninsula. This should yield a considerable number of species not included thus far in our lists.

SUB-ORDER ARACHNOMORPHAE

AMAURORIIDAE

Amaurobius americanus (Emerton). — Several immature specimens which probably belong to this species. Albion, May 5, 1929.

AGELENIDAE

Coras medicinalis (Hentz). — A common and widely distributed species in the United States and southern Canada. Washtenaw Co., Oct. 22, 1921; Albion, April 3, 8, 21, 1929; Homer, July 29, 1930; Swain's Lake, Sept., 1930.

Wadotes hybridus (Emerton). — Listed by Chamberlin (1925) from New York, New Hampshire, and Massachusetts. Ann Arbor, 1921 (?).

PISAURIDAE

Dolomedes urinator Hentz. — A widely distributed species. Bishop (1924) states that it is uncommon in the North. In a pool, Albion, July 7, 1930.

Pisaurina brevipes (Emerton). — Hitherto listed from Massachusetts, Ontario, Ohio, and Michigan. We have it from Ann Arbor, Nov. 6, 1921, and Albion, June 7, 1930.

LYCOSIDAE

Schizocosa saltatrix (Hentz). — Heretofore reported from New York and New Jersey southward to Georgia and westward to Kansas and Texas. One specimen found in moss, Albion, May 25, 1929.

OXYOPIDAE

Oxyopes salticus Hentz. — This is a species found all the way from Michigan and Long Island, New York, southward through the West Indies, Mexico, Central America, and northern South America. Also reported from the Pacific Coast of the United States. Our one specimen is from near Shelby, Oceana Co.

SICARIIDAE

Scytodes thoracica (Latreille). — Probably introduced from Europe. Now spread over much of the United States east of the Mississippi River. Recently found in Toronto, Canada. Albion, 1930 (?); Pentwater, Oceana Co., July 7, 1931.

THERIDIIDAE

Euryopis funebris (Hentz). — Distributed from southern Canada, including the Rocky Mountains, through all parts of the United States to Mexico. Homer, July 29, 1930.

Theridion murarium Emerton. — This is a common species in southern Canada as far west as British Columbia. Emerton (1919) states that it is "the most common fence Theridion." Common also in New England and New York and as far west as Colorado, Arizona, and Washington (Worley and Pickwell, 1931). We have but one specimen, Albion, 1930 (?).

PHOLCIDAE

Pholcus phalangioides (Fuesslin). — This remarkable spider is truly cosmopolitan, being known from nearly all parts of North America, much of South America and Europe, Asia, and Africa. In this country it has been regarded as an importation, but it has likewise been so regarded in Europe. Its original home is difficult to determine. From laboratory workroom, Albion, Feb. 14, 1929.

LINYPHIIDAE

Hypselistes florens (Cambridge). — Probably occurs all over southern Canada and the United States. Only from Washtenaw Co., Nov. 6, 1921.

Lephthyphantes minutus (Blackwall). — So far as known to us, this species and the following species are the only members of the genus occurring in the north. Both are European. *L. minutus* is probably found only in the eastern half of the country, whereas *L. nebulosus* occurs all over the United

States. Albion, Oct. 1, 1929, Sept. 10, 1930; Olivet, Eaton Co., July 17, 1930.

Lephthyphantes nebulosus (Sundevall). — Washteñaw Co., Oct. 27, 1920; Albion, July, 1930.

ULOBORIDAE

Uloborus americanus Walckenaer. — Known from southern Ontario throughout the United States, West Indies, Mexico, and much of Central America. Albion, July 14, 1931.

ARGIOPIDAE

Araneus pratensis (Hentz). — A widely distributed species, but apparently not common in this region. Crosby (1926) does not list it among the species of New York. Washtenaw Co., Aug. 2, 1916.

Araneus sericatus Clerck. — A common species in the vicinity of Albion and widely distributed over the whole country, much of Canada, and Europe. Albion, June 1, July 26, Aug. 8, 1930, Aug. 1, 27, Nov. 23, 1931; Oceana Co., July, 1930.

Larinia borealis Banks. — Formerly reported from New York, the Atlantic Coast, Washington state, and a few other places. Probably widespread over the country. On grass and weeds, Albion, Sept. 23, 1930.

Pachygnatha brevis Keyserling. — Known from southeastern Canada and many of the eastern states. One specimen found in a pitcher plant, Montcalm Lake, Albion, May 2, 1931.

Tetragnatha caudata Emerton. — Seeley (1928) states that this species "is distributed from Canada to Florida and west to Minnesota." "It is a water-loving species" and seems to be rather rare. This spider is usually known as *Eucta caudata* or *E. lacerta*. Olivet, Sept. 13, 1929; Albion, July 31, 1930.

Tetragnatha pallescens Cambridge. — Seeley (1928) says of this species: "This seems to be an uncommon but widely distributed species. Specimens in our collection are few and take in the area from New York to Florida and Porto Rico, west to Minnesota and Missouri. Banks reports it from

Lower California." Ann Arbor, 1921 (?); Montcalm Lake, Albion, June 27, 1930; Bath Mills, Albion, Aug. 5, 1931.

Tetragnatha vermiformis Emerton. — This spider has been called both Eucta and Eugnatha very commonly. Probably it is well distributed over the region east of the Rocky Mountains, although Seeley (1928) gives a more restricted range. Two specimens, probably from Albion, 1930, but data uncertain.

DRASSIDAE

Drassodes robustus (Emerton). — One immature female seems to belong to this species. Under bark, Albion, March 3, 1929.

Sergiolus montanus (Emerton). — Described from New England, but now seems to occur westward to the Pacific Coast. Ann Arbor, 1921.

THOMISIDAE

We are indebted to W. J. Gertsch, University of Minnesota, for the identification of all of the following Thomisidae except the first species and *P. lineatus*.

Misumenoides aleatorius (Hentz). — Listed by Petrunkevitch (1911) as occurring in all states and Canada. Albion, July 2, 1928, June 18, 1931.

Oxyptila conspurcata Thorell. — Probably occurs throughout the northern United States and southern Canada. One mature male and an immature female. Albion, June 2, 1931.

Philodromus lineatus Emerton. — Hitherto known from New England and New York. Not common. Albion, Oct. 1, 1929, June 27, 1931.

Tibellus maritimus M. — According to a personal communication from Gertsch, this is a rather rare European spider, which is found over most of the northern United States. Bath Mills, Albion, Aug. 5, 1931.

Xysticus banksi Gertsch. — This is *Coriarachne versicolor* of Emerton (1902) and Comstock (1912), or *Xysticus versicolor* of Petrunkevitch (1911). Widely distributed in the United States and Canada. Common in the vicinity of Albion. Al-

bion, Oct. 28, 1928, March 12, March 28, April 8, 1929; Berrien Center, July 8, 1931.

Xysticus discursans Keyserling. — A western and southwestern species. One female, Albion, 1930.

Xysticus elegans Keyserling. — Shelby, July, 1930.

Xysticus funestus Keyserling. — Albion, Oct. 1, 1929, Sept. 10, 1930, Aug. 15, 1931.

Xysticus graminis Emerton. — Albion, July 9, 1929.

Xysticus gulosus Keyserling. — From southern Canada throughout the United States. Albion, Sept. 23, 26, 1929, Sept. 23, Oct. 5, 1930.

CLUBIONIDAE

Anyphaena rubra Emerton. — Known from the northeastern states, westward to Kansas. *A. gracilis* (Hentz) is considered synonymous with this species by Worley and Pickwell (1931). Albion, 1931 (?).

Clubiona tibialis Emerton. — Apparently one of the less common *Clubionae*, distributed along the Atlantic seacoast and westward into the Middle West. Winnipeg Lake, Albion, July 14, 1931.

Trachelas tranquillus (Hentz). — A common species throughout the United States. Ann Arbor, Oct. 13, 1921; Albion, Oct. 25 and 28, 1929; July, 1930.

ATTIDAE

Icius hartii Emerton. — Known from Quebec and New England westward to Nebraska. Albion, July, 1931.

Icius similis Banks. — From British Columbia and most of the United States. Shelby, Oceana Co., July, 1930; Albion, June 27, 1931.

Maevia vittata (Hentz). — Occurs from southeastern Ontario throughout the United States. Albion, June 28, 1930.

Marpissa undata (De Geer). — From Nova Scotia, all states, Mexico, and Guatemala. Albion, Sept. 26, 1929; Olivet, July 27, 1931.

Metaphidippus montanus Emerton. — This is a species which

seems to be characteristic of mountainous regions. It has been found in northern Ontario, New Hampshire, and North Carolina. Albion, June 21, 1930.

Neon nellii Peckham. — Known from Ontario and many of the northern states. This is the smallest member of the Attidae in our fauna. Shelby, July, 1930.

Phidippus audax (Hentz). — Known from Canada and almost the entire United States. Ann Arbor, Oct., 1917; Albion, July 13, 1928, June 13, 1930, July 14, Sept. 6, 1931; Berrien Center, July, 1931.

Phlegra fasciata (Hahn). — Found in Massachusetts, Alabama, Indiana, Michigan, and Texas. Shelby, July, 1930.

Salticus scenicus (Clerck). — A European form which is common over much of North America, living on buildings, fences, etc. Albion, Feb., 1929, June, July, 1930; Berrien Springs, July, 1931.

Wala palmarum (Hentz). — Distributed over the eastern third of the country. Albion, Sept. 6, 1930.

Zygoballus bettini Peckham. — Much more widely distributed than the following species, having been reported from a large number of the states of the United States. Homer, July 29, 1930; Olivet, July 27, 1931.

Zygoballus nervosus (Peckham). — Known from New England, New York, Virginia, and Middle Western states. Albion, July 3, 1930.

Albion College
Albion, Michigan

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SPERMATOGENESIS IN THE BELOSTOMATIDAE. IV

MULTIPLE CHROMOSOMES IN *LETHOCERUS*

ARTHUR M. CHICKERING AND BARBARA BACORN

THE study of the male germ cells in the Belostomatidae has been continued by the senior author for a number of years. In the local species known to us as *Lethocerus americanus* Leidy eight chromosomes are present in the spermatogonia. Six of these are autosomes; two constitute a typical XY-pair of sex-chromosomes (Chickering, 1927). All of the eight chromosomes behave as expected in other similar cases. In *L. uhleri* (Montd.) from New Orleans (Chickering, 1931) there are probably thirty chromosomes present in each spermatogonium, among which there is also an XY-pair of sex-chromosomes. The suggestion has been made that the chromosome complex characteristic of *L. uhleri* has been derived by fragmentation of the eight chromosomes of *L. americanus*. Mixed with *L. americanus* and thus far indistinguishable from it have been found certain male specimens with an extremely interesting chromosome complex clearly to be interpreted as a case of multiple chromosomes. The present study has been made in an effort to understand the structure and behavior of the multiple chromosomes in this unnamed variety or species of *Lethocerus*. It is well known that the somatic differences in this genus are obscure, and that the whole question of classification is in an unsatisfactory condition. We hope, therefore, to be able to help somewhat in accomplishing a more satisfactory taxonomic treatment of the genus than is possible at the present time.

Multiple chromosomes have been observed and studied since the early part of the century (De Sinety, 1901; Mottier, 1903). The studies of McClung (1905, 1917) have added greatly to the

understanding of the phenomenon. Multiple chromosomes are found more commonly in Orthoptera, but have been observed in a considerable number of genera, in which they appear in various forms. The multiples found in *Choabrus plumicornis* (Frolowa, 1929) somewhat resemble those found in *Lethocerus*. In this species of *Choabrus* the X- and Y-chromosomes are always closely attached to an autosomal pair except in somatic prophases and spermatogonial resting nuclei, in which they are free. They also appear separate for a short period before the tetrads reach the equatorial plate for the first maturation division. When they appear unattached they take the form of a deeply stained, compact pair.

Various fixing fluids and stains were used in the preparation of the *Lethocerus* material studied. Most of the work has been done on sections. These observations have been supplemented, however, with work on smears.

The numerous spermatogonia very clearly show four large chromosomes paired according to shape and size. Two are reniform bodies; two are sigmoid (Fig. 58). In this stage no indications have been seen of the X- and Y-chromosomes which are so clearly shown in all other known Belostomatidae. For reasons which will appear later, however, each of the single chromosomes of this stage probably consists of two units joined end to end.

The exact time when the two compact elements interpreted as an XY-pair become separate in each nucleus is uncertain, but in the synizesis stage these can be clearly seen as condensed, rounded bodies lying close together. From this time until a late stage in the condensation of tetrads the identity of these two small bodies can be clearly traced.

Throughout the pachytene and diplotene stages the apparent XY-pair remains in nearly the same condition as when it is first seen in synizesis. As the nuclei go over into the diffuse stage, the sex-chromosomes stand out very clearly in contrast to the remainder of the chromatin, which is very lightly stained. The similarity between the appearance of these bodies and the sex-chromosomes of other species makes their recognition at this time practically certain.

As the chromosomes emerge from the confused stage, masses of chromatin appear, and soon darkly stained threads condense from these masses. It is during this time that evidence of multiple chromosomes becomes definitely established. One tetrad gradually emerges from the diffuse stage in the form of two double threads attached at one end. At this time the sex-chromosomes are clearly visible as dyads attached to the free ends of the homologous threads (Fig. 59). The octad resulting from this method of union condenses until it appears at metaphase as two darkly stained, longitudinally split bodies attached end to end. The relations of different parts of the other octad group are evidently much closer. In this case the early octad appears as a closed ate-

Fig. 58

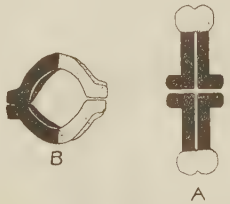

Fig. 59

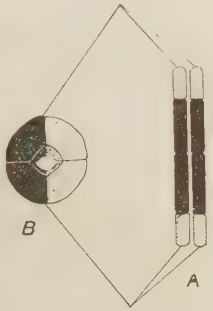

Fig. 60

Fig. 58. Spermatogonial chromosomes. Multiple attachment is probably end to end, but places of union are not visible

Fig. 59. Early octads. Sex-chromosomes stippled in multiple *A*. In multiple *B* the probable arrangement of the units is shown diagrammatically

Fig. 60. Metaphase of first division showing further condensation of octads

lomitic ring (Fig. 59). There should be definite breaks in the ring indicating the position of the units of the multiple, but these have not yet been seen. Further evidence, however, points to what must occur at this stage. The closed ring condenses into two very darkly stained, reniform bodies which lie attached at metaphase in such a manner that a thick, ringlike formation is assumed. The first division separates the halves of each octad (Fig. 60).

The interkinesis stage is the most interesting and possibly the most significant of the whole maturation process. In late telophase of the first division and prophase of the second, a rearrange-

ment of relative position of the elements within each body takes place. After the first division the two dyad elements are probably arranged in end-to-end union (Fig. 61). In order that proper distribution of chromosome elements in each group may take

Fig. 61

Fig. 62

Fig. 61. Telophase of first division

Fig. 62. Interkinesis, showing the early behavior of the double dyads

place, the relative position of these must be changed. In multiple *A* (containing the sex-chromosomes) the quadruple body opens into a diamond-shaped figure, with the two monads forming each half of it (Fig. 62 *A*). Condensation of the figure occurs, so that one autosome and one sex-chromosome lie side by side. The two double groups then form a tetrad-

Fig. 63

Fig. 64

Fig. 65

Fig. 63. Later interkinesis, showing the later behavior of the double dyads

Fig. 64. Metaphase of second maturation division, showing how the double dyads simulate tetrads

Fig. 65. Four "chromosomes" which each spermatid is believed to receive

like figure (Fig. 63 *A*). These figures are clearly visible in our preparations and have been very puzzling to interpret. On the other hand, they seem to lead inevitably to an explanation such as we have offered here.

Multiple *B*, a quadruple, reniform body opens outward, so

that the two groups containing opposing elements of each multiple are separated. The group appears as two curved bodies attached at the middle point of their convex surfaces (Fig. 62 *B*). The figure further condenses, so that we again see a body which closely simulates a rodlike tetrad of simple design (Fig. 63 *B*).

Both groups simulate tetrads in metaphase, and divide in similar fashion at the second division (Fig. 64). In all cases each spermatid appears to receive four monads grouped in two pairs (Fig. 65).

After the second division the spermatids are rapidly organized and the haploid nuclei are formed. For a considerable period organization of the spermatid nucleus takes place in which the chromatin material is clearly grouped into four loose masses, one of which is often smaller than the others. At this stage the spermatid nuclei closely resemble those of *L. americanus*, in which the number of chromosomes is clearly four. This is interpreted as additional evidence that we are in reality here dealing with multiple chromosomes in essentially the manner in which we have outlined their relationships.

Albion College
Albion, Michigan

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LAND MOLLUSKS FROM THE ISLANDS OF MINDORO AND LUBANG, PHILIPPINES

WILLIAM J. CLENCH AND ALLAN F. ARCHER

THIS paper is based upon a series of fine material sent to us by Señor Pedro de Mesa of Calapán, Mindoro, Philippine Islands. It is not complete for the smaller forms, few of which have been received. Some records from Lubang Island, which were not included in our former paper, are now inserted.[1] In the main this paper deals with northern Mindoro (see Map 2). The area considered lies north of Mambúrao on the west coast and Nauján Lake near the east coast. The fauna of the central and southern areas is still but imperfectly known.

Mindoro lies almost directly south of Batangas Province, Luzon, Philippines. It is a mountainous island whose greatest length from Bulalacao to Calavite Point is about 110 miles. Like several of the larger islands of the Philippines, it has a more or less peculiar molluscan fauna, which bears some resemblances to certain forms of southern Luzon on the one hand and to forms of the Busuanga Islands on the other. The genus *Camaena* is here characterized by the section *Phoenicobius*. The most peculiar forms are seen in the development of the genus *Helicostyla*, whose sections *Prochilus* and *Chrysallis* are practically limited to Mindoro. The other sections of *Helicostyla* are more like those of southern Luzon.

The additional records for Lubang are as follows:

20. *Trochomorpha beckiana* Pfr. — Lubang.

21. *Eulota fodiens subbolus* 'Nev.' Mllf. — Lubang: Cabra Island.

22. *Chloraea bifasciata dealbata* Mllf. — Lubang: Tagbac; Cabra Island.

[1] *Occ. Pap. Boston Soc. Nat. Hist.*, 5 (1931): 333–339.

Map 2. Sketch map of Mindoro, Philippine Islands, giving principal collecting localities

23. **Chloraea thersites vigoensis,** var. nov. (Pl. LVII, Figs. 4–5).

Description. — Shell imperforate, lens-shaped, rather thin. Nuclear whorl bluish black; succeeding whorls characterized by a broad spiral band covering two thirds of each whorl, at first light brown, but gradually becoming a deep chestnut brown. Four fifths of the basal area a deep chestnut color; rest of the shell ivory-yellow. Peristome white; parietal callus, very thin, and transparent, so that the characteristic basal coloring is continued inside the aperture. Whorls 3; body whorl sharply carinated except the latter half behind the aperture, where it is much compressed; nuclear whorl flattened, succeeding whorls broad and flat. Peristome flat, sharp-edged, expanded especially at the peripheral area, but at the basal area adnate as far as the parietal wall; columella flat, extremely short and slightly expanded inwardly. Sculpture consisting of axial striae, cut across by microscopic spiral lines.

Altitude	Greater diameter	Lesser diameter	
13.5 mm.	32 mm.	24 mm.	Holotype

Holotype. — Mus. Comp. Zoöl., No. 81384. Monte Vigo, Lubang; Pedro de Mesa, collector.

Remarks. — This form, of which we have but a single specimen, differs from *Chloraea thersites* Brod. in having a broad, dark, spiral band, a more depressed spire, and a greater compression on the body whorl.

24. *Cyclophorus appendiculatus* Pfr. — Lubang.

The remaining portion of this paper deals with Mindoro.

1. *Leptopoma concinnum* (Del.) Sby. — Mayabig; Bacó; San Teodoro.

2. *Leptopoma helicoides* Grat. — Bacó; San Teodoro.

3. *Cyclophorus appendiculatus recidivus* Mllf. — Calapán; Bacó.

4. *Cyclophorus fernandezi* Hid. — Calapán; Bacó; San Teodoro; Tara Mangyan, Abra de Ilog.

The specimens from Bacó and San Teodoro are lighter colored and stouter than those from Calapán.

5. *Ennea bicolor* Hutton. — Calapán.

6. *Rhysota* (*Lamarckiella*) *muelleri* Pfr. — Calapán; Karayrayan, Bacó; San Teodoro.

7. *Rhysota* (*Lamarckiella*) *muelleri planata* Mllf. — Monte Amatang, Abra de Ilog; Palúan; Calawagan, Palúan.

By reason of these records this variety is now established as coming from northwestern Mindoro.

8. *Rhysota* (*Rhysota*) *ovum* Val. — Naujan; Ariaod; Mt. Sapol, Calapán.

One specimen received from Ariaod is of the typical blackish color, but is larger than the typical form.

9. *Camaena* (*Phoenicobius*) *brachyodon* Sby. — Calapán; San Teodoro.

10. *Camaena* (*Phoenicobius*) *brachyodon naujanica* Hid. — Calapán; San Teodoro; Dulangan.

This variety intergrades with *C. brachyodon* Sby. Some specimens agree with *C. brachyodon naujanica* in shape, but possess the columellar teeth characteristic of the straight species.

11. *Camaena* (*Phoenicobius*) *oblonga* Sby. — Bacó.

12. *Camaena* (*Phoenicobius*) *oömorpha* Sby. — Tara Mangyan, Abra de Ilog.

13. *Camaena* (*Phoenicobius*) *oömorpha diminuta* 'Mllf.' Semper. — Puerto Galera.

The form of the variety found here is tawny yellow, but otherwise it agrees with Semper's figure (*Reisen in Arch. Phil.*, 10 [1906]: 45; Pl. 9, Figs. 10-10 *a*). Previously, according to von Möllendorff, it was known only from southwestern Mindoro.

14. *Obba listeri* Gray. — Ariaod; Calapán; Bacó.

15. *Obba planulata* Lam. — Anduyanan, Palúan; Mambúrao.

The specimens from Mambúrao have a light, indistinct pattern, and probably represent a transition to the following variety.

16. *Obba planulata sarcochroa* Pils. — Between Palúan and Mambúrao; Palúan.

It is not surprising that in *O. planulata*, which is widely spread in the central Philippines, the same types of variation should crop out in many separated regions. Originally described from Luzon, this variety is represented here by specimens which possess spires slightly more depressed than those of the typical form. It is interesting to note that the shells of some of these animals are more or less covered with algae, a condition which occurs as well with *Caracolus sagemon* Beck of Cuba.

17. *Chloritis* (*Trichochloritis*) *brevidens* Sby. — Mayabig; Ariaod.

18. *Chloraea constricta* Pfr. — Tara Mangyan, Abra de Ilog.

Specimens from this locality have light brown bands instead of the typical dark chestnut. In one individual of the series the bands are fused, giving it an extraordinary resemblance to *Coryda alauda* Fér. of Cuba.

19. *Chloraea thersites* Brod. — Ariaod; Mt. Sapol, Calapán; Calapán; San Teodoro.

20. *Helicostyla* (*Calocochlea*) *melanochila* Val. — Near Nauján Lake; Mt. Sapol, Calapán; Calapán; Karayrayan, Bacó; San Teodoro; Dulangan, Puerto Galera; Tara Mangyan, Abra de Ilog.

One lot received from Dulangan consists of two malformed specimens, quite depressed, with a broad, flat body whorl and a wide, flaring aperture.

21. **Helicostyla** (**Calocochlea**) **monacha,** sp. nov. (Pl. LVII, Fig. 1).

Description. — Shell imperforate, globose, rather solid. Nuclear whorl ivory-yellow, which continues onward to the edge of the peristome and becomes slightly tinged with brown. From the nuclear whorl onward a subsutural dark brown band, at first very narrow, but gradually widening; from the first whorl succeeding the nuclear whorl onward a supersutural dark brown band, at first very slight, but rather rapidly widening until it develops into a

strong band above the periphery of the body whorl. Just below the periphery of the body whorl an ivory-yellow band covered most of the way by a thick cartridge-buff zone of hydrophanous cuticle; below the subperipheral yellow band a broad dark brown zone covering most of the base, but interrupted near the columella by another yellowish band, and inside that a dark brown circumcolumellar band. Body whorl suffused by a rather light hydrophanous cuticle ornamented by spiral lines at irregular distances from one another, these in turn being cut across by rather faint axial lines. As already mentioned, there is a subperipheral band of hydrophanous cuticle. Peristome blackish brown; columella white; aperture white; whorls 4, only slightly convex, body whorl keeled; spire rather flat; peristome narrow, rounded, slightly reflected, slightly recurved; columella broad, flat, and rather straight, slanting at 111° angle from the basal lip inward toward the parietal wall; parietal callus thin; aperture dome-shaped; suture very slightly impressed. Sculpture consisting of closely crowded axial striae, cut across by spiral lines, which are especially common below the periphery of the body whorl.

Altitude	Diameter	Aperture height	Aperture width	
33.5 mm.	39.5 mm.	17.5 mm.	16.5 mm.	Holotype

Holotype. — Mus. Comp. Zoöl., No. 81353. Binuañgan, Palúan, Mindoro, P. I.; Pedro de Mesa, collector.

Remarks. — This species is readily distinguishable from *H. melanochila* by its keel and its higher spire. The stronger development of spiral lines is another difference. Its lighter color, especially on the spire, and scantier hydrophanous cuticle are other distinguishing characteristics. It also has a stronger columella. It is unique among the known Helicostylae of the section *Calocochlea* which occur in Mindoro in possessing a definite keel. The species is probably rare; only one specimen is known.

22. *Helicostyla* (*Calocochlea*) *roissyana* Fér. — Pinagbayanan; Binuañgan; Anduyanan; Calavite Pt., Palúan.

The specimens from Pinagbayanan are larger than the typical forms, and the basal area is broken up into two bands.

23. *Helicostyla* (*Calocochlea*) *roissyana cuticularis* Mllf. — Tara Mangyan, Abra de Ilog; Anduyanan and Calawagan, Palúan.

Walter F. Webb of Rochester has distributed specimens of this variety with Calintaan, Mindoro, as the locality. They are lighter than the typical, with subsutural flecks.

24. **Helicostyla** (**Calocochlea**) **roissyana bartschi,** var. nov. (Pl. LVII, Fig. 2).

Description. — Shell imperforate, globose-turbinate, thick. Nuclear whorl ochraceous buff shading off into chestnut brown on the two succeeding whorls. A short distance below the suture the latter color in turn resolves itself into a band 2 mm. wide, and gradually disappears beneath the hydrophanous cuticle on the last two thirds of the body whorl. From the end of the nuclear whorl onward a gradually widening subsutural band appears, at first light brown, but soon merging into black. Beginning at the first two and one-quarter whorls after the nuclear whorl a slight supersutural brownish band gradually widening and merging into black, until on the body whorl it develops into a broad zone above the periphery. A band 3 mm. wide, light yellow or white (when the cuticle is absent), is produced just below the periphery. Basal coloring black; peristome purplish black except at the peripheral area, where the white of the interior of the aperture continues almost to the edge; basicolumellar area washed by dark purple; columella white; subsutural band overlaid by a whitish, hydrophanous cuticle. Body whorl overlain by a dark gray, hydrophanous cuticle which is, however, absent on parietal and circumcolumellar area; whorls 5, rounded, gradually increasing. Spire high but flattened on the top; aperture oblique; peristome rather narrow, and sharply but narrowly reflected; columella slanting inward from the base, flat, wide, merging sharply into the parietal wall in an umbilical depression; parietal callus thin; suture moderately impressed. Sculpture consisting of numerous irregularly spaced lines or folds; nuclear whorl almost devoid of lines, and frequently weathered; hydrophanous cuticle cut up by irregularly spaced, wavy, threadlike lines.

Holotype. — Mus. Comp. Zoöl., No. 81365. *Paratypes.* —

Mus. Comp. Zoöl., No. 81352 Anduyanan, Palúan, Mindoro, P. I.; Pedro de Mesa, collector.

Altitude	Diameter	Aperture height	Aperture width	
33.5 mm.	37 mm.	20 mm.	16 mm.	Holotype
33	34	17	15	Paratype
32	33.5	16	14.5	Paratype
35	35	19	16	Paratype
31.5	33	17	14.5	Paratype

Remarks. — This variety is one of the most distinct forms of *H. roissyana* yet encountered, for it differs definitely from the straight species. At first glance, indeed, it would almost seem to be a different species. The typical yellow coloring of the spiral area is here replaced by a deep chestnut brown. The solid black basal color and the very broad, black superperipheral zone contrast with the peripheral band and the frequently light-colored superperipheral area of *H. roissyana.* The darkish hydrophanous cuticle of *H. roissyana bartschi* is not often found in the straight species. The spire is higher, although even those specimens most closely approximating *H. roissyana* in shape are also high-spired. It must, of course, be admitted that none of the northern Mindoro series of *H. roissyana* are identical with the typical form.

Additional locality. — Binuangan, Palúan.

25. **Helicostyla** (**Calocochlea**) **aopta,** sp. nov. (Pl. LVII, Fig. 3).

Description. — Shell imperforate, globose, rather solid. Nuclear whorl white, gradually shading off into darkish, dull yellow on the body whorl. From the nuclear whorl onward a brownish red subsutural band; from about one and one-half whorls from the nuclear whorl a reddish, gradually widening, gradually darkening band situated a short distance above the suture and continuing as a superperipheral band on the body whorl; a broad, brownish band on the body whorl just below the periphery. A brown circumcolumellar band present; aperture white; peristome and columella white; a slight hydrophanous cuticle appearing on the body whorl in the form of axial streaks cutting across the bands. Whorls 4, rounded, gradually increasing, and quite broad in back of the peristome; spire somewhat elevated; aperture broadly

oblique and open; peristome rounded, moderately expanded and recurved; columella broad, slanting from the basicolumellar region sharply inward toward the parietal wall; parietal callus extremely thin; suture moderately impressed. Sculpture consisting of crowded axial folds or lines, indistinct on the nuclear whorl, but gradually becoming plainer beyond that area.

Altitude	Diameter	Aperture height	Aperture width	
35.5 mm.	39.5 mm.	21 mm.	20 mm.	Holotype

Holotype. — Mus. Comp. Zoöl., No. 81354. Between Puerto Galera and San Teodoro, Mindoro, P. I.; Pedro de Mesa, collector.

Remarks. — This interesting new species is unfortunately represented by but a single specimen. It has hitherto been overlooked and may be quite rare. It bears a resemblance to several species from Luzon. It seems closest to *H. persimilis* Fér. It is a duller yellow with lighter bands and a narrower peristome, and is more depressed, having wider whorls.

26. *Helicostyla* (*Helicostyla*) *fulgens* Sby. — Nauján; Mt. Sapol, Calapán; Calapán; San Teodoro.

27. *Helicostyla* (*Orthostylus*) *pithogaster* Fér. — Mt. Sapol, Calapán.

It is curious that this species of Luzon and the neighboring islands occurs in both Lubang and Mindoro. It is rare in both regions. Possibly it has been distributed, as have certain other Philippine land shells, by the intervention of man. In this case, however, one would expect to find it about the city of Calapán rather than on a mountain some distance away.

28. *Helicostyla* (*Prochilus*) *virgata* Jay. — Ariaod, Nauján; Calapán; San Teodoro; Saklag.

29. *Helicostyla* (*Prochilus*) *virgata pulchrior* Pils. — Ariaod, Nauján; San Teodoro.

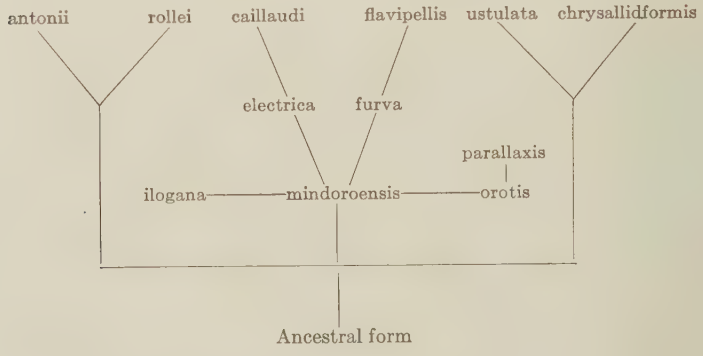
30. *Helicostyla* (*Prochilus*) *virgata porracea* Jay. — Ariod, Nauján; Calapán; San Teodoro; Saklag.

31. *Heliscostyla* (*Eudoxus*) *virginea* Lea. — Karayrayan, Bacó; Dulangan.

The presence of this species in Ilocos, Luzon, as well as in Catanduanes, gives it a scattered and discontinuous distribution. The specimens from Mindoro do not differ from those from Catanduanes. It is possible that this species has been distributed by man, and that Catanduanes is its original home, for the only other form closely related to it (*H. virginea bustoi* Hid.) also occurs there.

32. *Helicostyla* (*Chrysallis*) *mindoroensis* Brod. — Mayabig, Bacó; Calapán; San Teodoro; Tara Mangyan, Abra de Ilog; Calomintao.

This species is evidently limited to the north coast. The section *Chrysallis*, of which it is a member, occurs only on Mindoro. It is perhaps a recent development of *Helicostyla*, for it is still in a plastic condition. A large series of specimens of the various species of *Chrysallis* show that the separation between them is not very great. Many specimens from a single lot exhibit definite variations in shape. A hypothetical table of relationships, based on the material at hand, is given below:



33. *Helicostyla* (*Chrysallis*) *mindoroensis electrica* Rve. — Calapán; San Teodoro; Calomintao.

This form has been considered a species separate from *H. mindoroensis*, but a large number of specimens show that these forms apparently intergrade. It is advisable to consider it a variety. Reeve [2] states that its main difference is in color pattern. Pilsbry (*Man. of Conch.*, Ser. 2, 8 [1892]: 54) further differentiates this variety, stating that the parietal callus is porcelain-white edged with brown. This characteristic appears in many specimens, but not consistently in all examples. Specimens of *H. mindoroensis* at hand have a light-colored cuticle similar to that in *H. mindoroensis electrica*. In general, it may be said that the shape of the shell is alike in both forms, and that *electrica* has a light-colored spire and a lighter periostracum. *Helicostyla mindoroensis caillaudi* Petit (*Journ. de Conch.*, 1 [1850], Pl. 13, Fig. 3) is a valid variety. It is plain yellow, with a reddish periostracum, and is a light-colored form of *H. mindoroensis*, agreeing with it in size and shape.

34. **Helicostyla (Chrysallis) mindoroensis ilogana,** var. nov. (Pl. LVIII, Fig. 4).

Description. — Shell openly and rather deeply perforate, oblong-ovate, rather thick. Nuclear whorl whitish yellow or slightly tinged with brown; succeeding whorls ivory-yellow, shading off into dark chestnut brown. From the first full whorl succeeding the nuclear whorl and for the next two or three whorls the subsutural region is ornamented with hydrophanous flecks at irregular intervals from one another, which in turn become streaks of hydrophanous cuticle farther on. These streaks become increasingly wider on the whorl succeeding the body whorl, until they almost fuse. This hydrophanous cuticle is light chestnut. On the body whorl the black ground color appears as a few irregular streaks. Interior of aperture very light blue; peristome purplish blue; parietal callus usually translucent, but slightly tinged with brown; whorls $5\frac{3}{4}$–6, slightly convex; spire obtuse; peristome rather broadly reflected, moderately thick, slightly re-

[2] *Bulimus mindoroensis*, Reeve, *Conch. Icon.*, 5 (1848), Pl. 5, Fig. 21.

curved; columella rather broad, slanting at an angle from the parietal wall away from the outer lip and toward the basal lip; parietal callus rather thin; aperture ovate or broadly ovate; suture slightly impressed. Sculpture as in *H. mindoroensis*, consisting of axial striae.

Altitude	Diameter	Aperture height	Aperture width	
56.5 mm.	33 mm.	24.5 mm.	14.5 mm.	Holotype
59	30.5	23.5	13	Paratype
55.5	30	24	13	Paratype
55	31.5	22.5	13.5	Paratype
50.5	28	22	13.5	Paratype

Holotype. — Mus. Comp. Zoöl., No. 81359. *Paratypes.* — Mus. Comp. Zoöl., No. 47264. Tara Mangyan, Abra de Ilog, Mindoro, P. I.; Pedro de Mesa, collector.

Remarks. — This variety is distinct from *H. mindoroensis* in color. The nuclear whorl is light instead of blue. The body whorl has the dense chestnut hydrophanous cuticle instead of the broad blackish streaks with the rather narrow flames. Although its light tip is like that of *H. mindoroensis*, it differs in general color. The latter has very nearly the same color as *mindoroensis* except that, as already noted, in some specimens the hydrophanous streaks are set wide apart and are zigzag. *H. m. ilogana* has a darker and thinner peristome than *H. m. electrica.*

Additional localities. — Camorong and Pt. Amatang, Abra de Ilog.

35. **Helicostyla (Chrysallis) mindoroensis furva,** var. nov. (Pl. LVIII, Fig. 3).

Description. — Shell rather narrowly umbilicate, elongate-ovate, slightly thick. Nuclear whorl grayish white; next three and one-half whorls chestnut; succeeding whorls progressively shading off into sooty black on the body whorl. First three whorls after the nuclear whorl ornamented by straw-colored subsutural flecks at fairly frequent intervals from one another. Succeeding whorls ornamented by rather wide, irregularly shaped, straw-colored or brownish yellow streaks which become rather zigzag-shaped below the periphery of body whorl, in some cases being so

broad that they become fused together. Peristome ebony; columella bluish white edged with ebony; parietal wall covered with a brownish callus; interior of aperture bluish white; whorls $5\frac{3}{4}$, slightly convex; periphery of body whorl in some specimens slightly carinated; spire obtuse; aperture subovate; peristome rather thin, broadly reflected, and slightly recurved; columella almost straight, slightly dilated inward, broad; parietal callus thin, transparent; suture slightly impressed. Sculpture from nuclear whorl onward consisting of closely placed axial lines or folds; nuclear whorl axially striated, next two or three whorls containing irregularly placed, spiral, incised lines cutting across the axial lines.

Altitude	Diameter	Aperture height	Aperture width	
50.5 mm.	25 mm.	22 mm.	12 mm.	Holotype
54.5	24	21.5	12	Paratype
52	26	22	13	Paratype
50.5	26	22	13	Paratype
47	24	20.5	11	Paratype

Holotype. — Mus. Comp. Zoöl., No. 81356. *Paralypes.* — Mus. Comp. Zoöl., No. 81355. Binuañgan, Palúan, Mindoro, P. I.; Pedro de Mesa, collector.

Remarks. — This variety from northwestern Mindoro is readily distinguished from *H. mindoroensis*. Its spire is chestnut instead of bluish black. On the body whorl the subperipheral area is lighter colored than in *mindoroensis*. Its cuticular streaks are lighter and stand out in greater contrast with the ground color. It has a more turned spire, and the body whorl is less convex, whereas the keel on the periphery is lacking in *mindoroensis*. It differs from *H. mindoroensis electrica* in having a darker spire and narrower and lighter axial streaks. The ground color is more in evidence on the body whorl. In general, the color pattern is different. The spire is more tumid, and the succeeding whorls are less convex. The atypical specimens of *electrica* from Tara Mangyan are closer in size, but contrast in color pattern.

Additional locality. — Camorong, Abra de Ilog, Mindoro, P. I. This form is more ovate and of lighter color than the typical form.

36. **Helicostyla (Chrysallis) mindoroensis flavipellis,** var. nov. (Pl. LVIII, Fig. 5).

Description. — Shell rather narrowly umbilicate, oblong-ovate, slightly thick. Nuclear whorl ivory-white, succeeding whorls light yellowish fawn, the depth of color increasing on the body whorl. Some specimens, beginning with the nuclear whorl, ornamented with light yellow axial streaks irregular in shape and becoming increasingly wide; other specimens have these only as subsutural flecks. Peristome tinged by very light, delicate pink, which continues on the columella; interior of aperture white; whorls 5–5¾, moderately convex; spire obtuse; peristome rather thin, moderately reflected, slightly recurved; columella moderately broad, rather straight; parietal callus thin; aperture ovate; suture somewhat impressed; nuclear whorl with delicate axial striae; succeeding whorls sculptured with closely crowded axial lines or folds.

Altitude	Diameter	Aperture height	Aperture width	
51 mm.	26 mm.	22.5 mm.	11.5 mm.	Holotype
57	26.5	24	11.5	Paratype
50	25	24	11	Paratype
51	26	24	12	Paratype

Holotype. — Mus. Comp. Zoöl., No. 81358. *Paratypes.* — Mus. Comp. Zoöl., No. 81357. Calawagan, Palúan, Mindoro, P. I.; Pedro de Mesa, collector.

Remarks. — This variety is probably an offshoot of the same stock as the preceding variety. It is distinguishable by its yellow color and its light-colored aperture and is exactly the same in shape, except that the peripheral keel is almost absent. When we first received specimens of this form, we thought them a form of *H. antonii* Semper. However, the whorls are less convex, the spire more tumid, and the aperture more angular. This form obviously belongs to the *H. mindoroensis* group. It is parallel to *H. mindoroensis caillaudi* Petit, but differs in several important respects. It is a much darker yellow. The peristome is lighter, whereas that of *caillaudi* is red-tinged. The nuclear whorl is more tumid; the whorls are more convex, and are shorter. The shell is about

10 mm. shorter. The actual locality of *H. mindoroensis caillaudi* is not known.

Additional locality. — Top of Mt. Calavite, Palúan, Mindoro, P. I. The form from this locality is very dark fawn-colored, with a light purplish peristome.

37. **Helicostyla (Chrysallis) mindoroensis orotis,** var. nov. (Pl. LVIII, Fig. 1).

Description. — Shell rather widely perforate, oblong-ovate, slightly thick. Nuclear whorl whitish fawn color, shading off into light chestnut on the succeeding whorls and persisting on the body whorl to the edge of the peristome; from the periphery of the body whorl to the base a broad zone of straw color or whitish yellow. Around the umbilicus a zone of dark brown showing also inside the aperture just at the top of the columella. From the nuclear whorl on a series of buff-yellow, subsutural, hydrophanous flecks, which become longitudinal streaks of hydrophanous cuticle on the latter whorls, although in many specimens missing below the periphery of the body whorl. Peristome light bluish purple, deepening on the outer edge; parietal callus transparent; aperture faintly exhibiting the color of the exterior; whorls 6, slightly convex; spire obtuse; peristome quite thin, rather broadly reflected, and somewhat recurved; columella moderately broad, straight, and slanting from the parietal wall away from the outer lip and toward the basal lip; parietal callus very thin; aperture ovate; suture very slightly impressed. Sculpture consisting of axial striae.

Altitude	Diameter	Aperture height	Aperture width	
52.5 mm.	26.5 mm.	23 mm.	13 mm.	Holotype
55	26	24	13	Paratype
52	25	21.5	12.5	Paratype
49.5	24	21	10.5	Paratype

Holotype. — Mus. Comp. Zoöl., No. 81360. *Paratypes.* — Mus. Comp. Zoöl., No. 81363. Near Calavite Mt., Binuañgan, Palúan, Mindoro, P. I.; Pedro de Mesa, collector.

Remarks. — This variety differs from *H. mindoroensis* and its

other varieties in being light chestnut in color with a straw-colored, subperipheral zone on the body whorl. All the other forms are quite dark. It is shaped very nearly the same as *H. m. furva*, although it has a wider umbilicus. Its more tumid spire contrasts with the smaller one of *mindoroensis*. At first glance this form would almost seem to be a distinct species. However, in shape it is exactly like the other varieties of *mindoroensis* that occur in the municipality of Palúan. Its chief difference is in color, and there it has departed no more from the usual than have certain other varieties of *mindoroensis*.

38. **Helicostyla (Chrysallis) mindoroensis parallaxis,** var. nov. (Pl. LVIII, Fig. 2).

Description. — Shell narrowly perforate, elongate-ovate, moderately thick. Nuclear whorl light ivory-yellow, shading off into chocolate-brown on the next three whorls, which in turn become very dark brown or dull black on the body whorl. Beginning at the end of the nuclear whorl a series of dull yellow, subsutural, hydrophanous flecks, which become longitudinal, irregularly spaced, often with zigzag brown streaks on the later whorls, and may nearly cover the entire surface of the body whorl. Peristome grayish blue; interior of aperture white; spire rather depressed; whorls $5\frac{1}{2}$–6; body whorl slightly angulate medially; succeeding whorls convex, rapidly descending to body whorl; aperture ovate; peristome thin, sharp, rather broadly reflected, slightly recurved; columella rather narrow at the base, but broadly and regularly expanding higher up; parietal callus thin, transparent. Sculpture consisting of slight, irregularly spaced axial lines, from the nuclear whorl onward.

Altitude	Diameter	Aperture height	Aperture width	
60.5 mm.	28 mm.	24 mm.	12.5 mm.	Holotype
57.5	24.5	22.5	12	Paratype
58	27	26	12.5	Paratype
55	26.5	23	12.5	Paratype
55	24	21	12	Paratype
54	24	22	12	Paratype

Holotype. — Mus. Comp. Zoöl., No. 83275. *Paratypes.* — Mus. Comp. Zoöl., No. 83726. Palúan, Mindoro, P. I.; Pedro de Mesa, collector.

Remarks. — This variety is abundant in northwestern Mindoro. Although it intergrades with *H. m. furva,* it is usually quite distinct. It is lighter colored, with straighter, less widely spaced zigzag stripes. The peristome is light blue instead of ebony, as in *furva.* The shell is more elongate, with a rather sharp angle at the juncture of the columella and the peristome, contrasting with the rounded base of *furva.* Its shape is most nearly like that of *H. m. orotis,* but is quite unlike it in its dark color. Nevertheless the two forms are closely related and come from the same region. It cannot be confused with *H. ustulata* Jay. It differs in its smaller size and fewer whorls, $5\frac{1}{2}$–6 instead of $6\frac{1}{4}$–7, as in *ustulata.* The whorls are less convex, the spire is less tumid, and the aperture is smaller proportionately and more ovate. The peristome is smaller and thinner and the umbilicus is narrower and the axial folds are lacking. Although these two forms exist side by side, yet their similarity in possessing unusually elongate shells is a parallelism, and is not indicative of close relationship. *H. ustulata* is evidently a distinct species belonging near *H. chrysallidiformis* Sby. rather than in the *H. mindoroensis* series.

Additional localities. — Camorong, Abra de Ilog; Mt. Calavite, Palúan.

39. *Helicostyla* (*Chrysallis*) *ustulata* Jay (Pl. LVIII, Fig. 6). — Camorong, Abra de Ilog; Palúan.

This species may have its metropolis in the interior of Mindoro. The five specimens sent by Señor de Mesa are unusually large ones (74 mm. long), with chestnut spires, brownish black streaks, and bluish black peristomes. Jay's [3] original figure of this species is very poor, but is recognizable. It is not clear whether he had dark specimens or lighter ones. Some specimens from older collections have a light chestnut ground color, contrasting with the specimens at hand, but this is possibly due to fading. Pilsbry,

[3] Jay, J. C., *Catalogue of Shells* (1839), p. 9, Pl. 6, Fig. 1.

Man. of Conch., Ser. 2, 7 (1892), p. 52, has considered *H. ustulata* a variety of *H. chrysallidiformis* Sby. The two forms are, however, distinct. *H. chrysallidiformis* is a light-colored derivative of the same stock. In general, it may be said that *H. ustulata* differs from *H. chrysallidiformis* in having a more tumid spire, less convex whorls, and a broader peristome. The aperture is shorter, and the umbilicus is wider. The suture is more impressed, and the prominent axial folds are less numerous and less crowded. As yet we have no definite locality records for *H. chrysallidiformis*, but it probably comes from the interior of Mindoro.

40. *Helicostyla (Chrysallis) rollei* Mllf. — Mayabig; Bacó; Mt. Halcón (type locality).

This species, hitherto rare in collections, has been furnished in satisfactory numbers by Señor de Mesa. It is primarily a species from the interior. It varies less from locality to locality than any other species of the section *Chrysallis*. *H. antonii* Semper is a derivative of the same stock. It belongs closer to *H. rollei* than to any other species, and is similar in shape, though having a more tenuous spire. It has a yellow periostracum and a white peristome. It is a species of the west-central portion of Mindoro.

41. *Opeas gracile* Hutton. — Calapán.

A tropicopolitan species.

42. *Auricula ponderosa* Pfr. — San Teodoro.

43. *Pythia reeviana* Pfr. — Punta Naganahao, Calapán.

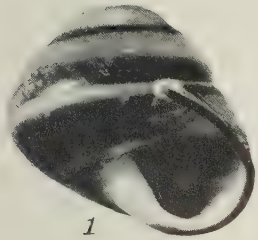
44. *Pythia cumingiana* Petit. — At San Teodoro River, San Teodoro.

45. *Melampus fasciatus* Desh. — Punta Naganahao, Calapán.

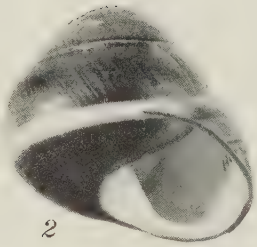
46. *Melampus caffer ater* A. Ad. — Bacó.

Museum of Comparative Zoölogy
Cambridge, Massachusetts

PLATE LVII



1



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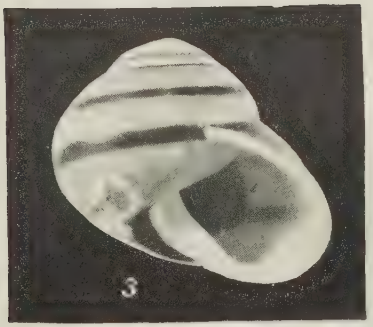

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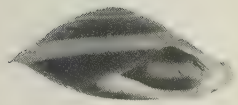

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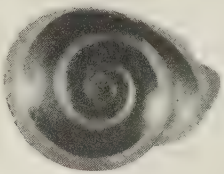

5

Fig. 1. *Helicostyla monacha* Clench & Archer
Fig. 2. *H. roissyana bartschi* Clench & Archer
Fig. 3. *H. aopta* Clench & Archer
Figs. 4–5. *Chloraea thersites vigoensis* Clench & Archer

All specimens are holotypes, Mus. Comp. Zoöl., Nos. 81353, 81365, 81354, 81384, respectively. Photographs by F. P. Orchard

PLATE LVIII

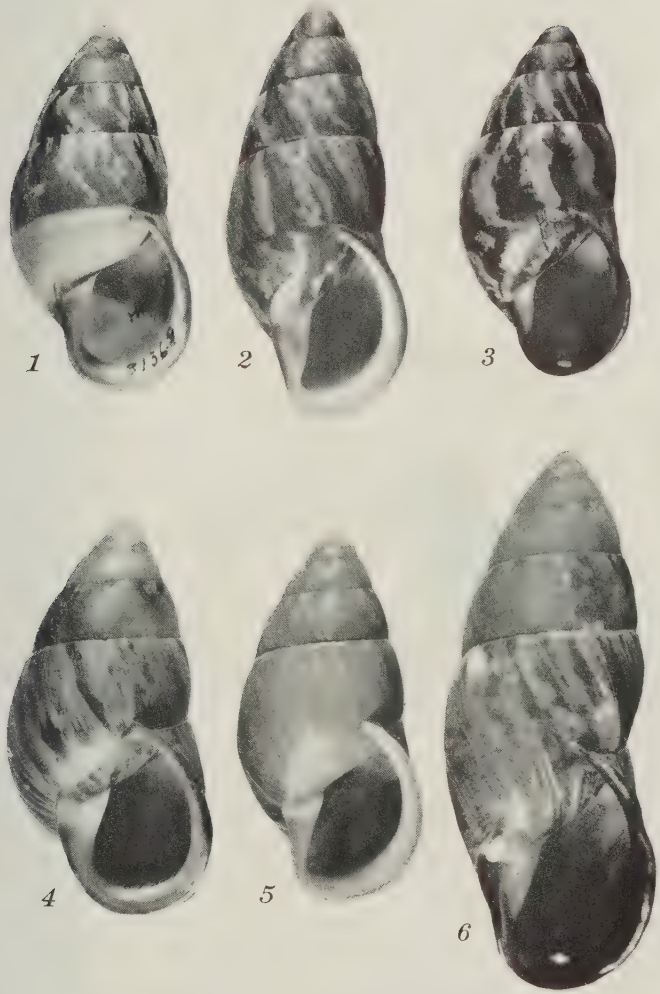

Fig. 1. *Helicostyla mindoroensis orotis* Clench & Archer
Fig. 2. *H. m. parallaxis* Clench & Archer
Fig. 3. *H. m. furva* Clench & Archer
Fig. 4. *H. m. ilogana* Clench & Archer
Fig. 5. *H. m. flavipellis* Clench & Archer
Fig. 6. *H. ustulata* Jay

Specimens 1–5 are holotypes, Mus. Comp. Zoöl., Nos. 81360, 83275, 81356, 81359, 81358, respectively. Photographs by F. P. Orchard

DISTRIBUTION OF THE FISHES IN THE INLAND LAKES OF MICHIGAN

THOMAS L. HANKINSON

THE small inland lakes of Michigan are well known for their scenic beauty and their recreational facilities, including fishing; but considering their value to biologists, few papers have resulted from the study of their biota. The animal and plant life of Douglas Lake in Cheboygan County, on which the Biological Station of the University of Michigan is located, has received more critical attention than any other Michigan lake, and a number of valuable papers have resulted. The ones that give most data on the life of the lake are by Reighard (1915), Colbert (1916), Hussey (1919), Jewell and Brown (1924), Smith (1924), Welch (1928), and Eggleton (1931). An intensive study of Walnut Lake, Oakland County, Michigan, was made by the writer (Hankinson, 1908), in association with Charles E. Davis and James G. Needham, both of whom contributed to the report (Davis, 1908; Needham, 1908). In his report on the mollusks of White Lake, Frank Collins Baker (1907) gives important data on one phase of the life of a small Michigan lake. Other contributions of similar importance are by Adams (1909), Shelford (1913), and Hubbs (1921, 1929). The State Board of Fish Commissioners of Michigan (1886) gives in its report lists of the fishes known from a large number of the inland lakes of the state.

The plants of inland lakes have received considerable attention from botanists (Davis, 1900, 1907, 1908; Reed, 1902; Pennington, 1906; Holt, 1909). Their data are very useful to zoölogists who are interested in the ecology of fishes and other animal life of these small bodies of water. The lakes of Michigan have been described from a physiographic viewpoint by

I. D. Scott (1921); this work is of fundamental importance to all biological investigations of the regions treated.

A directory of Michigan lakes, edited by H. W. Henshaw (1931), gives a list of 4,187 for the state, with names of the game fishes of each.

In the morainic region of northern Indiana, which is similar to that of Michigan, are many small lakes, investigations of some of which have yielded important information on the fishes and associated organisms (Eigenmann, 1896; Clark, 1902; Youse, 1902; Headlee and Simonton, 1904; Evermann and Clark, 1920; De Ryke, 1922; Scott, 1931). Contributions pertaining to the ichthyology of small glacial lakes have come from other regions neighboring Michigan: from Illinois, by Forbes and Richardson (1909); from Ontario, by Dymond (1926); and from Ohio by Detmers (1912). Forbes (1887) gives a useful general account of the interrelations of organisms in lakes, which is very helpful to students interested in the ecology of these bodies of water. In Wisconsin especially valuable contributions to inland-lake biology have been made by Wagner (1908), Birge and Juday (1911 and 1914), Pearse (1918, 1921, and with Achtenberg, 1920), and Cahn (1927).

In recent years considerable unpublished information on the fishes of the inland lakes of Michigan has accumulated. The Department of Conservation has been making many investigations of these waters. Dr. Jan Metzelaar, before his death in 1929, obtained abundant, important data which are not yet published. Through the coöperation of the Department of Conservation, the Izaak Walton League, and members of the University of Michigan there has been established the Institute for Fisheries Research, directed by Dr. Carl L. Hubbs, with headquarters at the Museum of Zoölogy of the University of Michigan. At present this Institute is following an extensive program of inland-lake investigations.

During the progress of my ichthyological studies, which began as early as 1905 in Michigan, I have become acquainted to a varying extent with the fish life of some forty inland lakes of Michigan, and, prior to 1900, as a boy angler I learned much

about the fishes of the lakes of Hillsdale County, Michigan, though my pursuits were not with scientific intentions. The information obtained in those juvenile days has proved of value in later studies.

It seems advisable to publish the essential data in my notes of inland lakes, for two reasons: (1) to show how little is really known concerning the distribution of fishes in them, thus making it easier for students to find problems for needed investigation; and (2) to produce a publication of some basic value for the studies that have recently been initiated by the Institute for Fisheries Research.

Most of the inland lakes considered in this paper are in the depressions in the glacial drift that covers the State of Michigan. Estuary lakes close to the Great Lake margins and lakelike expansions of rivers are not here treated with reference to fish life. A restriction is made to bodies of water usually small and located among hills and with small outlets or inlets. Many lakes or "tarns" (Davis, 1907, p. 116) are not connected with stream systems. Scott (1921), in discussing the inland lakes of Michigan, notes that they range from thirty-one square miles in area down to unnamed ponds, and that there are seventy in the Lower Peninsula that are more than a square mile in area. It has been estimated that inland lakes cover about a fiftieth of the total surface of Michigan. Over five thousand occur in the state, and there are many similar ones in Wisconsin, Minnesota, southern Ontario, northern Indiana, and a few in Ohio.

It is well known that in our inland lakes conditions that affect fish and other aquatic organisms are continually changing. Probably in all of them the amount of vegetation is increasing, and in some in which there is much shallow water, with hills or woods giving protection from wind so that there is little wave action, plant capture is very rapid (Pl. LX, Fig. 2). Within the memories of people living in Michigan, lakes have completely disappeared. The broad marsh about Sand Lake in Hillsdale County (Pl. LX, Fig. 1) is a plant encroachment formed almost entirely since 1900. Within thirty years I have seen a lake similar to the one shown in Plate LXI, Figure 1, disappear entirely. All

degrees of advance of plants into lakes may be seen by a person traveling about the state, from large clear lakes (Pl. LIX, Fig. 1), with relatively little vegetation, down to swamps and marshes with no open water. Stages are shown by illustrations (Pls. LIX–LXI). Bottom soil changes in character. An inlet may introduce at intervals considerable terrigenous material. The winds carry soil, leaves, and other objects into lakes, all of which contribute to deposits. Marl is becoming more and more abundant in many lakes. Forty years ago I was very familiar with some lakes in Hillsdale County which had extensive sandy shallows, but at present thick beds of marl everywhere cover the bottoms of the shallows. With continued addition of bottom material, including accumulations of muck from plant decay, our inland lakes are becoming shallower. It is thus evident that the conditions for fish life in them are continually changing. We know that the different species require different sets of living conditions — in other words, different habitats. Some species dwell in deep water, coming to the shallows at breeding times only; others live on marginal shoals, rarely if ever going to the deeper parts of the lake. Some prefer mud bottoms; others, sand; and still others, marl. The history of an inland lake shows, then, a succession of fish habitats determined principally by vegetation, soil, and conditions due to depth, and accompanied by a succession of fish faunas.

An attempt is made here to classify the fish habitats of inland lakes, with consideration primarily of conditions pertaining to vegetal and depth features. Use has been made of the classifications of conditions found in inland lakes by Shelford (1913), Reighard (1915), Muttkowski (1918), and Chapman (1931).

CLASSIFICATION OF FISH HABITATS

(The subdivisions are not discussed in detail in the text.)

I. Limnetic or aphytal region
   1. Epilimnion, the stratum above the thermocline
   2. Mesolimnion or thermocline
   3. Hypolimnion or profundum

II. Sublittoral or shell zone

III. Littoral or vegetation zone
  1. Marginal shallows
    a. Open or barren shallows
      (1) Sandy shallows
      (2) Marl bottom
      (3) Stony bottom
      (4) Muck bottom
    b. Vegetal shallows, with abundant plant life
      (1) Submerged aquatic plant growths
      (2) Emergent aquatic plants
        (a) Bulrush patch or zone
        (b) Water-lily zone
        (c) Sagittaria and Pontederia patches
        (d) Areas of diversified emergent plant life
  2. Deeper littoral or potamogeton zone

IV. Bordering-marsh or sedge zone

I. Limnetic or Aphytal Region

The part of the inland lake with deepest water and central location is called the "limnetic region." It extends out beyond the thirty-foot contour line — the depth where bottom plants disappear. Muttkowski (1918) has designated the region "aphytal," on account of the absence of vegetation. Owing to unequal heating, three quite distinct strata may be found in the limnetic region in summer. At the surface winds overturn the water to variable depths; thus the temperature is determined by that of the air. This layer is called the "epilimnion." Nearest the bottom of the lake is the "hypolimnion," which comprises the mass of undisturbed water with a temperature about that of maximum density, 4° Centigrade. Between the two layers is the "mesolimnion" or thermocline (Birge, 1903; Needham and Lloyd, 1916). Here there is a temperature transition between the relatively warm water of the epilimnion and the cold of the hypolimnion. This thermal stratification at the limnetic region produces three very distinct habitats for fish. In the epilimnion the water is warm and variably heated and disturbed. It differs in thickness in different lakes and at different times in the same one (Welch and Eggleton, 1932). In Douglas Lake it appears to be about forty feet on the average. Little thorough collecting of the fish of the limnetic region has been done, and few pro-

ductive observations have been made. By means of floating nets Dr. Hubbs has taken from Portage Lake near Ann Arbor, Michigan, a few species of fish, namely, common shiners,[1] spot-tail minnows, and pike perch. I once saw a large gar pike just under the ice over deep water (Hankinson, 1906). In the summer time many young fish school right at the surface; and often toward evening they may be seen disturbing it. Among them are the young silversides. Dr. Hubbs (1921) has discovered that in this species the young of the season live at the surface and over deep water only. Definite information on the fish life of the hypolimnion or profundum is lacking, for it is very difficult to make collections from there, especially of forms too small to get with a gill net or a set line. In *eutropic* lakes (Chapman, 1931, p. 305) oxygen is scant and near the bottom of the hypolimnion, absent. Such conditions exist in Douglas and Third Sister lakes (Eggleton, 1931). Walnut Lake (Hankinson, 1908) was found to be of the *oligotropic* type, that is, it had oxygen at the bottom of the hypolimnion. Fish dwell all through the deep-water region of such lakes, but we would not expect to find them at the bottom of the eutropic type; nevertheless, Pearse and Achtenberg (1920) found that perch do enter such regions and feed under anaërobic conditions and draw upon the oxygen of the swim bladder for breathing. We do not know to what extent other fish do this.

The species known from the hypolimnion are few, and we have little information on the number of each there. At Walnut Lake I found common whitefish and common suckers apparently abundant in water as deep as a hundred feet. It is known that lake herring dwell there, in some lakes in large numbers. Lake trout also live in the hypolimnion, where they may be caught by deep trolling. Reighard (1915, p. 245) notes five species taken to a depth of forty-five feet in Douglas Lake, as follows: common sucker, grass pike, small-mouth black bass, perch, and burbot.

The invertebrate animals of the limnetic region appear to be much better known than the vertebrates, and important contributions concerning the crustaceans, worms, insects, and other

[1] The scientific names of the species mentioned in this paper are given in the list of inland-lake fishes at the end.

minute forms of life of the deep-water region of inland lakes have been made by Needham (1908), Shelford (1913), Needham and Lloyd (1916), Muttkowski (1918), and Eggleton (1931).

II. Sublittoral or Shell Zone

No definite information is at hand concerning the fish population of the sublittoral zone; hence only brief attention will be given to it.

The zone is recognized and described by Muttkowski (1918). Chapman (1931, p. 339) notes its principal characteristics. It is around the margin of the limnetic region and bordering the littoral zone on the lakeward side; thus it is between the limnetic region and the potamogeton zone of the littoral zone.

Its bottom has typically a mixture of sand, mud, and shells, with vegetation absent or very scant, and with feeble and dying plants.

Little can be learned of its fish life. Reighard (1915), in discussing the deep-water community of Douglas Lake, notes that certain species of fish tend to live about the margin of the deep water or limnetic region, so that they no doubt belong to the fauna of the sublittoral; these are common suckers, grass pike, smallmouth black bass, perch, and possibly burbots.

III. Littoral or Vegetation Zone

The shallower water bordering the central, deeper limnetic region is called the "littoral zone." It extends from the shore line out to the maximum depth where abundant vegetation occurs; and this appears to be between twenty-five and thirty feet (Davis, 1907, p. 129; 1908, p. 225). Plants grow wherever possible in an inland lake and, as just noted, their distribution is limited by the depth. Water disturbance also affects the plant life of such a lake. Where there is considerable wave action plants do not thrive; there appear to be most favorable conditions for them in the parts of the littoral region where there is least movement of the water and of the bottom soil and where the water is from fifteen to twenty feet deep (Davis, 1908, p. 226). Expanses of inland lakes exposed to the action of winds, especially the prevailing

ones, and with shallow water, have no vegetation, or at best a scant growth; veritable submerged deserts are formed. Where hills or woods give protection to shallows, many plants ordinarily occur, often forming extensive, dense growths (Pl. LIX, Fig. 2).

The majority of the species of fish in the inland lakes seek the cover of plants in the littoral region. Here they find abundant food and favorable shelter, but there are some species that appear to avoid vegetation and that are adjusted to the barren, plantless waters; in fact, among the inland-lake species there are different degrees of preference for plant-covered areas. It is possible, therefore, to recognize rather distinct habitats for the different fishes of the lake, determined by the amount of vegetation present, depth of water, and other factors. An attempt to subdivide the littoral zone has resulted in recognizing two rather distinct habitats, called (1) the "marginal shallows," and (2) the "deep vegetal" or "potamogeton zone."

1. MARGINAL SHALLOWS

Where the exposure of the shore of an inland lake is such that wave action is strong and frequent and the soil is gravelly or sandy, the outwash from the shore builds up beds of sand, sometimes with intermixed clay or humus, more or less extensive and forming zones of shallow water with clean, plantless bottoms; these are the well-known bathing beaches of our inland lakes. They usually extend lakeward to a depth of five or six feet, where there is a decided drop-off to deep waters. These open shallows form distinct fish habitats and have distinct faunas.

There are two types of marginal shallows: (*a*) open or barren, with rooted plants scant or absent, and (*b*) vegetal, typically with abundant plants emergent and submergent.

a. Open or barren shallows

Shallow water with little or no plant life is found at parts of inland lakes exposed to winds. The wave action disturbs the bottom soil and thus prevents plants from becoming established. Sand or marl usually forms the bottom, but sometimes these wave-washed shallows have gravel or cobble bottoms, and muck

may be present near mouths of streams or along marshy borders. A number of subhabitats may thus be recognized. The following conditions are peculiar to the barren shallows: (1) instability of bottom material; (2) irregular disturbance of water, with a region of breaking waves near shore called the "rachion" (Muttkowski, 1918); (3) variable water temperature; (4) maximum illumination; (5) relatively large oxygen content of water; and (6) absence or scarcity of sheltering objects. The visibility of fish in the shallows betrays them to enemies such as herons, kingfishers, and water snakes. Only small species can dwell safely near shore; and they secure protection by the schooling habit and by rendering themselves inconspicuous through simulating the bottom color by varying the pigment display in the skin. They seek sheltering objects and gather about anchored boats, piers, and the like (Pl. LXII, Fig. 2).

Fishes abundantly represented on vegetation-free shallows are blunt-nosed minnows, straw-colored minnows, spot-tail minnows, mimic shiners, skipjacks, Menona killifish, and the young of silverfin minnows, small-mouth black bass, and perch. Where the bottom is quite stony, we find in addition to these species log perch and Johnny darters. This list applies to the more southern waters of Michigan in the eastern deciduous-forest region, but in the northern mixed-forest country there occur these same species, except skipjacks, which become scarce, and, in addition, black-nosed dace, long-nosed dace, trout perch, young common suckers, and lake chubs, and sometimes other species. Dr. Hubbs informs me that he has seen burbots under submerged objects in the open shallows. In a few lakes he found rainbow darters common on gravelly bottom. This species rarely occurs in bodies of water other than streams.

At night the larger fish of the pondweed zone come to the open shallows, where they may be seen with a light; occasionally in the daytime a bass of good size is observed in very shallow water, evidently after minnows; and families of bullheads, each composed of one or both parents with a compact school of hundreds of very small young ones, frequently form a conspicuous sight in shallow, open water.

As a spawning place for fish, the barren shallows do not appear to be extensively used. Bluegills come to nest in the deeper parts where the water is about three feet in depth, and colonies of many nests, each with its attending fish, form a common sight in early summer. Where stones, water-logged boards, pieces of bark, and similar objects are on the bottom, blunt-nosed minnows work beneath these objects and deposit their eggs on the lower side. At one time I found on the clean sands of a good bathing beach a discarded, leaky milk pail in which was a pair of yellow bullheads, with a big mass of eggs, which they were attending, so that there is something favorable to be said of the untidy cottager who in throwing junk into shallow water may create a home for some fish. With a view to increasing the numbers of fish in our inland lakes the Institute for Fisheries Research is at present experimenting to learn results of introducing in the shallows of deep lakes objects that will furnish breeding places for useful forage fish like the blunt-nosed minnow.

b. Vegetal shallows, with abundant plant life

Where lake shallows are out of the line of prevailing winds or protected from them by shore features such as hills, woods, and buildings, there is so little disturbance of bottom soil that plants get an easy foothold and often become abundant, producing prominent vegetal conditions or "weedy" shallows. Even where there is considerable wave wash, plants, especially bulrushes, gradually encroach upon the barren shallows, and even these regions are doomed to plant capture in time. At vegetal shallows we then find all degrees of density of plant growth from scant patches to those so choked that there are no swimming places for fish.

Plants of the shallow waters are submerged or emerged. Prominent among the latter are bulrushes, which in many lakes form extensive and often dense zones of cat-tails, arrowheads, pickerel weeds, and water lilies (Pl. LXIII, Fig. 1). Common submerged plants are stoneworts, often forming extensive and thick carpets, pondweeds of several species, tape grass, hornwort, water weed, water milfoil, bladderworts, and slender naiads. Information concerning the species and the general character of

inland-lake vegetation may be obtained from a number of publications (Davis, 1900, 1907, 1908; Hankinson, 1908; Reighard, 1915; Colbert, 1917; Evermann and Clark, 1920; Rickett, 1920; Ackley, 1932; Oosting, 1932).

The plants growing in the shallows furnish fish with a considerable amount of insect and other invertebrate animal food and with abundant shelter, and they form the principal breeding habitat of species of inland-lake fish. The bulrush zone, on account of its providing good concealment and being in deeper water than other growths of emerged aquatic plants, is considerably used by nesting fish. I have found common sunfish, green sunfish, long-eared sunfish, large-mouth black bass, and rock bass nesting in the rush zone. It is known that dogfish, chub suckers, carp, golden shiners, blunt-nosed minnows, common bullheads, yellow bullheads, tadpole cats, and skipjacks breed on the vegetal shallows, and no doubt many other species, the breeding habitats of which are little known, also breed there.

The vegetal shallows constitute the principal feeding ground of the young of the inland-lake fishes and an important feeding place of the following species: common suckers (in northern lakes), chub suckers, yellow bullheads, common bullheads, perch, large-mouth black bass, rock bass, green sunfish, long-eared sunfish, and common sunfish. There are some small species that live almost continually in and about thick vegetation after this appears in the summer. Characteristic forms are the fine-scaled dace of northern lakes, northern red-bellied dace, black-chinned minnows, silvery minnows, pug-nosed shiners, black-nosed shiners, mud minnows, black-banded top minnows, mud pickerel, Iowa darters, least darters, and the nine-spined sticklebacks of northern lakes. Nearly all the fish with a preference for the open shallows occur at times where there are plant growths, and most of them have a tendency to congregate near them. Some species appear to be equally at home in either situation, such as blunt-nosed minnows, spot-tail minnows, fatheaded minnows, lake chubs, black-nosed shiners, mimic shiners, northern dace, log perch, and skipjacks. The skipjack is, however, a surface form, apparently little influenced by bottom features.

Pond lilies (Pl. LXIII, Fig. 1), which form broad and conspicuous zones in many inland lakes, furnish effective shelter and a good feeding place for large numbers of fish. Anglers know this and often cast their hooks in and about them to get bass or pickerel in ambush among the lily pads.

2. DEEPER LITTORAL OR POTAMOGETON ZONE

The deeper part of the littoral zone, in water from about six to twenty-five feet deep, where there is minimum wave disturbance, has an abundance of submerged vegetation. Members of the genus *Potamogeton* are especially abundant in this part of the lake.

The plants of the potamogeton zone are well known to botanists and are treated by Davis (1908), Moore (1915), Evermann and Clark (1920), and Oosting (1932). No intensive studies of the ecology of this zone have been made.

The pondweed zone is undoubtedly the most important fish habitat of the inland lakes, at least for the larger, adult fish. Clear proof of its importance is the presence of many anglers in boats anchored over it, noticeable on almost any summer day. Favorable features of this zone are as follows: (1) It is usually very extensive, commonly with a large area where the water ranges in depth from six to thirty feet; (2) The depth of the water and the tall plants furnish good concealment from enemies; (3) There is an abundance of invertebrate animal life feeding on the plants and providing food for the fish (Moore, 1915); (4) It is favorable as a hunting ground or region of ambush for the larger, fish-eating species, such as gar pike, grass pike, and the black basses. They prey on the smaller fish living in the pondweed zone or on those of the marginal shallows that venture out into the deeper waters where plants grow. Excursions are made into the bordering shallow waters of the lake from the pondweed zone by the large predators, especially at night; and the zone gives them a convenient and safe place for retreat.

The most common and characteristic species and the ones that spend most of their lives in the zone, according to our present knowledge, are as follows: dogfish, chub suckers, black-chinned minnows, golden shiners, common bullheads, yellow bullheads,

grass pike, large-mouth black bass, warmouth bass, bluegill, green sunfish, common sunfish, black crappies. Not many collections of small fish have been made from the pondweed zone, but it is evident that they occur there in large numbers, for we know that at times they disappear from the shallows and, very probably, go no farther out into the lake than the pondweed zone, but a more thorough study of the small fish of the limnetic region may show that they do go still farther out, at least in oligotropic lakes. At Walnut Lake, with the use of a water glass, I could see large numbers of blunt-nosed minnows, Johnny darters, and other small species in eight or ten feet of water. It is probable that during late fall and winter the fishes in the pondweed zone in summer migrate to the deepest waters of our lakes. The fall overturn of lake waters would bring oxygen to these deep regions, eliminating a distinct hypolimnion and producing a region where fish could live during winter. It is known, according to Dr. Hubbs, that bluegills move out to the limnetic region in the late fall. By fishing through the ice I have found that perch, bullheads, and large-mouth black bass remain in ten or fifteen feet of water in large numbers through the winter.

IV. Bordering-Marsh or Sedge Zone

Shore features of our inland lakes are quite diversified. In places the water adjoins uplands (Pl. LXII, Fig. 1), and elsewhere there may be low, nearly level, broad, sandy or gravelly beaches. Features such as swamps, marshes (Pls. LX–LXI), and woods affect fish life indirectly, and sometimes directly, by furnishing insect food (Evermann and Clark, 1920), but when the waters of a bordering swamp or marsh are continuous with those of a lake, fish can enter these places, which become distinct habitats for them. I have observed many small fish moving about sedge clumps, where the vegetation made it impossible to collect and identify them. In a marsh bordering an inland lake in northern Washtenaw County, Michigan, on June 22, 1932, I was able, after considerable effort, to obtain a number of small fish. Many very young mud minnows were taken along with minute pickerel, and some advanced young of large-mouth black bass, warmouth

bass, long-eared sunfish, and chub suckers. The sedge zone is no doubt the home of mud minnows, which are known to live under marsh and swamp conditions (Gill, 1904).

The sedge zone is the breeding place for grass pikes, which come to this region very early in the spring. Immense individuals are sometimes seen splashing around with backs out of water while spawning and laying eggs.

The many kinds of sedges, grasses, and other plants of the sedge zone as found at Walnut Lake, Oakland County, Michigan, are treated by Davis (1908, p. 223); and descriptions of the vegetation for other inland lakes are given by Davis (1900, 1907), Reed (1902), Dawson (1911), and Evermann and Clark (1920).

The muskrat is a dynamic ecological factor influencing the fish and other life of the sedge zone by cutting vegetation, making huts about which are moatlike channels, and wearing runways all through the marshes.

LIST OF FISHES KNOWN TO OCCUR IN THE INLAND LAKES OF MICHIGAN, WITH SUMMER DIURNAL HABITATS INDICATED

The list of inland-lake fishes is built up through the examination of collections made by the writer, which have been principally from shallow water, and also through the card records of the much more extensive collections of small lake fishes preserved at the Museum of Zoölogy, University of Michigan, Ann Arbor. Direct observation has contributed to some extent. No doubt there will be more additions to the list in the near future on account of the active work on the inland lakes of Michigan now being done by the members of the Institute for Fisheries Research.

Published records have been consulted for data on occurrence and habitat; the papers found especially useful are as follows: Ruthven (1906), Hankinson (1906, 1908, 1916), Forbes and Richardson (1909), Reighard (1915), Evermann and Clark (1920), and Dymond (1926).

The terminology of Hubbs and Greene (1928) has been followed, except for later revisions of names.

The habitats where each species is known to occur are indicated by letters, as follows:

E = epilimnion
H = hypolimnion
L = limnetic region
O = open or barren shallows
P = potamogeton zone
S = sedge zone
Sl = sublittoral
V = vegetal shallows

An asterisk (*) is used when the preferred habitat is apparent. Letters italicized indicate the habitats of the young of the species.

Lepisosteus platostomus Rafinesque, Short-nosed gar	L P* V
Lepisosteus osseus (Linnaeus), Long-nosed gar	L P* O *V*
Amia calva Linnaeus, Dogfish	P* V
Leucichthys artedi (Le Sueur), Lake herring	H* P O
Fifteen or more subspecies of *artedi* have been recognized by ichthyologists from specimens from inland lakes (Koelz, 1931). All appear to have similar habitats in such lakes.	
Coregonus clupeaformis (Mitchill), Common whitefish	H* P O
Five subspecies among inland-lake whitefish have been recognized (Koelz, 1931).	
Salmo fario Linnaeus, German brown trout	P V
Salmo irideus Gibbons, Rainbow trout	P
Salvelinus fontinalis (Mitchill), Brook trout	H* P V
Cristivomer namaycush (Walbaum), Lake trout	H* P
Catostomus commersonnii commersonnii (Lacépède), Common sucker	H* Sl P O
Catostomus catostomus (Forster), Northern sucker	O
Hypentelium nigricans Le Sueur, Hog sucker	V P
Erimyzon sucetta kennerlii (Girard), Chub sucker	P *V*
Moxostoma erythrurum Rafmesque, Common mullet	*V*
Cyprinus carpio Linnaeus, Carp	P* *V* S
Couesius plumbeus (Agassiz), Lake chub	L P V O
Rhinichthys atronasus meleagris Agassiz, Black-nosed dace	O
Semotilus atromaculatus atromaculatus (Mitchill), Creek chub	V O
Margariscus margarita nachtriebi (Cox), Northern dace	V O
Pfrille neogaeus (Cope), Fine-scaled dace	V* O
Notropis heterodon heterodon (Cope), Black-chinned minnow	P V
Notropis anogenus Forbes, Pug-nosed shiner, Black-nosed shiner	V
Notropis heterolepis Eigenmann & Eigenmann, Black-nosed shiner	V* O
Notropis deliciosus stramineus (Cope), Straw-colored minnow	O

Notropis volucellus volucellus (Cope), Mimic shiner	V	*O*			
Notropis hudsonius hudsonius (Clinton), Spot-tail minnow	O*	*V*			
Notropis hudsonius selene (Jordan), Northern spot-tail minnow	P	O*	V		
Notropis whipplii spilopterus (Cope), Silverfin minnow	*O*				
Notropis atherinoides Rafinesque, Lake shiner	O				
Notropis rubellus (Agassiz), Rosy-faced minnow	O				
Notropis cornutus chrysocephalus Rafinesque, Common shiner	O	V			
Notropis cornutus frontalis (Agassiz), Common shiner	L	O*			
Notemigonus crysoleucas crysoleucas (Mitchill), Golden shiner	P	*V**			
Hybognathus hankinsoni Hubbs, Silvery minnow	V				
Chrosomus cos Cope, Northern red-bellied dace	V				
Hyborhynchus notatus (Rafinesque), Blunt-nosed minnow	P	O*	V		
Pimephales promelas promelas (Rafinesque), Fatheaded minnow	V*	O			
Campostoma anomalum (Rafinesque) Stone-roller minnow	O	P			
Ameiurus melas (Rafinesque) Black bullhead	P	*V*			
Ameiurus nebulosus (Le Sueur), Common bullhead	P*	V	*O*		
Ameiurus natalis (Le Sueur), Yellow bullhead	*V*	P*			
Schilbeodes gyrinus (Mitchill), Tadpole cat	V				
Schilbeodes miurus (Jordan), Brindled stonecat	O				
Umbra limi (Kirtland), Mud minnow	P*	V	*S*		
Esox vermiculatus Le Sueur, Mud pickerel	P	V*	S		
Esox lucius Linnaeus, Grass pike	L	Sl	P*	S	
Esox masquinongy masquinongy Mitchill, Muskellunge	P	*V*			
Anguilla bostoniensis (Le Sueur), Eel	P				
Fundulus diaphanus menona Jordan & Copeland, Menona killifish	*O*				
Fundulus dispar (Agassiz), Black-cheeked top minnow	V				
Fundulus notatus (Rafinesque), Black-banded top minnow	V				
Percopsis omiscomaycus (Walbaum), Trout perch	P	O			
Aphredoderus sayanus (Gilliams), Pirate perch	V				
Lepibema chrysops (Rafinesque), White bass	P				
Perca flavescens Mitchill, Perch	H	Sl	P*	*V*	*O*
Stizostedion vitreum (Mitchill), Pike perch	L	P*			
Percina caprodes semifasciata (De Kay), Log perch	P	O	V		
Ammocrypta pellucida (Baird), Sand darter	O				
Boleosoma nigrum nigrum (Rafinesque), Johnny darter	P	O	V		
Poecilichthys caeruleus caeruleus (Storer), Rainbow darter	O*	V			
Poecilichthys exilis (Girard), Iowa darter	O	V			
Catonotus flabellaris flabellaris (Rafinesque), Fan-tailed darter	O				
Microperca punctulata Putnam, Least darter	O	V*			
Micropterus dolomieu Lacépède, Small-mouth black bass	Sl	P*	*O*	V	
Aplites salmoides (Lacépède) Large-mouth black bass	L	P*	*V*	O	
Chaenobryttus gulosus (Cuvier & Valenciennes), Warmouth bass	P*	V	S		
Apomotis cyanellus (Rafinesque), Green sunfish	P*	V			
Helioperca incisor (Cuvier & Valenciennes), Bluegill sunfish	P*	V	O		

Xenotis megalotis peltastes (Cope), Long-eared sunfish	P	V*		
Eupomotis gibbosus (Linnaeus), Common sunfish	P*	V		
Ambloplites rupestris (Rafinesque), Rock bass	P	*V*		
Pomoxis sparoides (Lacépède) Calico bass	L	P*		
Labidesthes sicculus (Cope), Skipjack	E	P	O*	V
Eucalia inconstans (Kirtland), Brook stickleback	P	V	S	
Pungitius pungitius (Linnaeus), Nine-spined stickleback	P	V		
Lota maculosa (Le Sueur), Common burbot	H*	P	O	

CONCLUSIONS

Each species of fish in our inland lakes seeks a set of conditions favorable for it, called its habitat, and different species require different habitats; those of some are very restricted. The sand darter, for example, lives only on clean, sandy bottoms; the skipjack dwells close to the water surface, and the mud minnow is found only where vegetation is dense. Other species, such as perch and blunt-nosed minnows, live under a wide variety of environmental conditions.

The vegetal, bottom, and depth conditions in our inland lakes are continually changing through the encroachments of marsh and other marginal vegetation, the destruction of water plants by muskrats, and the increase of marl and terrigenous deposits. Favorable habitats for some species, therefore, are disappearing and for others improving. Certain fishes, then, are increasing and others decreasing; one predominating at one time, and another at another time. This accounts in part for the varying success attained by anglers. Sometimes a particular species obtains some big advantage over others and is represented considerably in excess of all others. I have known lakes where each of the following species greatly predominated over all others: perch, green sunfish, calico bass, and grass pikes. Such faunal fluctuations make it impossible to predict through mere superficial observations of an inland lake the presence of certain species there or the success of artificial introduction of a kind of fish desired. Each lake must be studied carefully and treated as a distinct problem.

The potamogeton zone is the principal abode of the larger species of fish in the inland lakes, and it is used as a retreat by the smaller fish that dwell in the marginal shallows. Thorough

ecological studies, with especial attention to the relations between the plants and fish, are needed (Moore, 1915). Important problems appear with reference to the effects of the different species upon one another and their interrelations with associated animals such as water birds, turtles, and the small invertebrate animals eaten by fish or living as parasites upon them.

There is a scarcity of information regarding the use of the limnetic region of inland lakes by fish. Only a few species are known to occur there, but it is possible that many enter the region, especially after the fall overturn of the waters. More deep-water collections are needed.

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Michigan State Normal College
Ypsilanti, Michigan

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FIG. 1. Silver Lake, Washtenaw County, Michigan. A morainic lake of moderate size, being about a mile in diameter. There is considerable wave action, and plant capture is progressing slowly. Littoral and limnetic regions distinct

FIG. 2. West Lake, Washtenaw County, Michigan. An extensive littoral region with abundant plant growth. Plant capture is rapid

PLATE LX

Fig. 1. Sand Lake, Hillsdale County, Michigan. A broad surrounding marsh is rapidly encroaching on the lake; most of the marsh or sedge zone has formed during the last thirty years

Fig. 2. A small lake in Hillsdale County, Michigan. Plant capture is rapid because of protection from wind by woods and hills. There is a distinct sedge and water lily zone

FIG. 1. A small lake of about an acre in Dexter Township, Washtenaw County, Michigan. Late stages of plant capture are shown. A very broad marsh or sedge zone surrounds the lake

FIG. 2. Details of shore features of lake shown in Figure 1. Sedge, water lily, and swamp loosestrife (*Decodon verticillatus* (L.) Ell.) are prominent

FIG. 1. Clear Lake, Jackson County, Michigan. An eroding shore adjoining barren shallows of a morainic lake

FIG. 2. Another view of barren shallows shown in Figure 1. Hundreds of small shoal fish had gathered for shelter under and about the bathers' float, where the water is about eighteen inches deep

FIG. 1. McCormick Lake, Washtenaw County, Michigan. Details of zone showing water lily and swamp loosestrife (*Decodon verticillatus* (L.) Ell.)

FIG. 2. Frain's Lake, Washtenaw County, Michigan, showing bordering sedge zone

OBSERVATIONS ON THE FLIGHT OF FISHES, WITH A STATISTICAL STUDY OF THE FLIGHT OF THE CYPSELURINAE AND REMARKS ON THE EVOLUTION OF THE FLIGHT OF FISHES

CARL L. HUBBS

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I. INTRODUCTION

PERHAPS too much ink has already been used in discussing the flight of fishes. Certainly too much of what has been written has been unduly deductive. Many have argued from preconceived ideas of the flight of birds, or from generally erroneous conceptions of the mechanics of flight, just how fishes must fly. A few

hours of close observation of fishes flying would often have shown the resulting deductions to be erroneous. No attempt is made in this paper to review the very extensive, though mostly incidental and trivial, literature on the flight of fishes. This has in part been done by Ahlborn (1895), Gill (1905), Hankin (1914), and others. A large but by no means complete list of references is indexed in Dean's *Bibliography of Fishes*.

Few of those who have written on the flight of fishes have made really critical field studies. Realizing this regrettable fact and being already interested in the subject (Hubbs, 1918; quoted by Nichols and Breder, 1928), I naturally took advantage of extremely favorable opportunities in 1929 to make some detailed studies.

Some of my observations of that year were made in the East and South China seas, about western Java, and around the entire main island of Japan, but most of the studies were carried out during the first half of June, when I chanced to journey from Java through Java Sea, Straits of Macassar, Celebes Sea, among the Philippine Islands, and on to southern Japan. The small size of the steamer on which the trip was made and its slow speed of only eight to ten knots were very favorable for observations. Still more fortunate was the circumstance that most of the seas traversed were exceptionally calm, usually with a glassy surface scarcely perturbed even by a ground swell. The details of flight were then very easily observed and tabulated. We had, however, enough rough weather to make possible a statistical study of flight over stormy as contrasted with calm seas. After we passed out from the Philippines into the open Pacific, the sea became increasingly rough as the wind developed into a gale.

Some of the observations were made by the unaided eye, but a larger number, including most of those on the positions of the fins at the various stages of flight, were made with the aid of good binoculars, which were continually kept at hand. The timing of flights was accomplished rather crudely, since there was no stop watch on board, by recording the number of ticks of an ordinary watch elapsing while a fish was in the air. Seemingly practical arrangements to measure the length of flights by the

simultaneous use of two sextants were made too late, for the sea had then become too rough to carry out the observations.

The extreme abundance of flying fishes in the calm seas and straits of southeastern Asia and their moderate though decreasing abundance in the open ocean provided ample material for the study. On day after day thousands of individuals, often singly, often in flocks, rose near the ship to sail away, in plain sight from a vantage point on the navigation deck.

By the rarest good fortune there once rose at very close range a school of that most primitive of flying fishes, *Oxyporhamphus* [*Evolantia*] *micropterus*, the flight of which has never been recorded. Several times the two-winged or monoplane flying fishes, *Exocoetus* proper, flitted out into observability. But by far the greatest number of observations were made on the four-winged or biplane flying fishes, the Cypselurinae. This is the group which, among fishes, has attained the ultimate in flight.

These observations on the flight of the true flying fishes (Exocoetidae) were supplemented by a few views of the air movements of *Tylosurus* and *Hemiramphus*, which belong to the same general group Synentognathi, but are more primitive than the Exocoetidae. The air leaps of such fishes as the tuna (*Thunnus*) and mullet (*Mugil*) were also seen.

Of the many thousands of fishes which I have observed in real flight, not one was suspected of belonging to any family other than the Exocoetidae. Certainly none was a "flying" gurnard (Dactylopteridae), another type of marine fish still held by some to be capable of flight (most recently by Beebe, 1928*a*, 1928*b*). I was, however, within the range of that family and obtained a considerable number of specimens. On my own brief negative observations I lay no great stress, but I am deeply impressed by the opinion of Lo Bianco, which has been quoted by several of the writers on the flight of fishes. This man, the famous collector and preparator of the Naples Zoölogical Station, after a lifetime of field work in the Gulf of Naples, where *Dactylopterus* is common, emphatically denied that this fish ever flies. He claimed it to be (as adult) essentially a bottom fish, and all its characters confirm this view.

Scrutinizing the massive bony helmet with long spines, the thick scales, unspecialized caudal fin, the highly modified dorsal and pelvic fins, and the detached hooklike pectoral lobe of Dactylopteridae, I find nothing even to suggest that these fishes could possibly attain the consummate speed necessary to hurl their heavy, ungainly bodies for any distance through the air. It is true that the pectoral fins of the dactylopterids, like those of the scorpaenoid *Pterois volitans*, are so immense as to give one on casual inspection the idea that these fishes can fly. But a critical investigation shows that these great pectoral fins could not possibly maintain so heavy a body in the air. They are so flexible that they will support the body horizontally between them only when they are grasped very close to their bases. Their outer portions are positively raglike. The thin, exserted, unbranched pectoral rays, graduated and unthickened and unsharpened along what would have to be the sharp, strong cutting edge of the plane if these fishes really could fly, contrast sharply with the structure of the pectoral rays in the Exocoetidae. The pectoral of the "flying" gurnard may well sustain the body weight in the dense medium of water, when the fish volplanes downward, as Beebe describes it as doing, but it is assuredly utterly insufficient to hold the fish in the air, even for a moment. Möbius' claim (1878), that he had seen *Dactylopterus* supporting itself in air by taut and non-vibrating wings was, therefore, erroneous. The flight of the "flying" gurnard may, I believe, be confidently added to the long list of sea myths.

The only structure in *Dactylopterus*, except the expanded pectorals, which has been held as adapted to flying is the air bladder (Calderwood, 1891). But it seems clear that this structure is particularly designed as a sound-producing organ. Its dorsal position I would relate rather to the constriction of the coelom by the body armature than to any aërostatic function. In regarding the heavy muscular wall of the air bladder as adapted to a sudden release of external pressure when the fish leaves the water, the author quoted must have forgotten his physics.

Sailors' yarns aside, nearly all the claims that dactylopterids fly seem to rest chiefly on Moseley's (1879, p. 571) observations,

which were made on the *Challenger* Expedition. Moseley thought he recognized species of "flying gurnets" in the air, supporting themselves grasshopper-like by buzzing their wings. But he observed small fish, which probably did not have greatly enlarged pectorals. How he could have made quite sure of the flapping of such tiny "wings" while its bearer dashed for an instant out of the water, I cannot understand. Though he claimed that he chased and caught one or two, he netted the fish out of the sargasso weed. I suppose that he chased a young flying fish and saw it alight near a mass of weeds, but failed to see it dart away, as is the habit of such fish; then netted a gurnard out of the vegetation and thus fooled himself and hundreds of others into believing that such a fish can fly, and that it does fly by buzzing its wings!

Flight has also been attributed to certain fresh-water fishes. The African butterfly fish, *Pantodon*, has almost as little in body form or fin structure to suggest real flight as has the "flying" gurnard. I know of no actual record of observations on its flight, although it has often been kept in aquaria (as is attested by numerous articles in aquarium journals). The statement or guess of one French explorer that *Pantodon* is a "petit poisson volant," expressed on a label in an exhibit in Paris, and the statement of another French explorer that he had observed a small flying fish about Lake Chad, appear to be the only bases for the hundred-times repeated claim that this fish can fly. This traveler's description of the air movements of *Pantodon*, repeated by Pellegrin (1906), along with a fanciful picture of the fish in activity which seems quite out of harmony with its form, is very brief and indicates some form of skimming rather that flight. The account states that the pectorals beat the water surface, which would seem to indicate that the fish does not leave the water, although we certainly have no reason to think that an untrained observer could see the individual fin movements. There is, furthermore, no proof or even good indication that the fish observed was a *Pantodon* rather than, as would seem more probable, a characin. Certainly there is no good reason to align *Pantodon* among the flying fishes.

The South American "fresh-water flying fishes," characins of

the subfamily Gasteropelecinae, are reputed by means of an actual flapping of the "wings," to accomplish their well-authenticated long skimming movements and short flights. The structure of these fishes, especially of their muscles, as Ridewood (1913) has pointed out, very strongly supports these observations.

Flight has also been accredited to certain fossil fishes (Landois, 1894; Abel, 1906, 1912; Lull, 1906; Young, 1915). On this question I have nothing to say.

II. THE FLIGHT OF THE MOST PRIMITIVE FLYING FISH

No observation has been published on the flight of *Oxyporhamphus*[1] *micropterus*, which is of critical interest because this rare species is apparently the most primitive of all the flying fishes, certainly the least specialized in respect to wing development. It was, therefore, a piece of real good fortune that I saw a flock of about twenty-five adult individuals of this genus take a flight in Bohol Strait, Philippine Islands, on June 7.

They rose near the boat, in fact almost below me and only 10 meters distant, and made away at right angles with the boat. They flew only 5 to 8 meters and rose but a few decimeters above the surface. Possibly with a longer start beneath the surface they would have flown farther, but they cannot be regarded as capable of really long soars. They merely volplaned like other flying fishes, for the pectorals were clearly neither flapped nor vibrated, even at the start of the short air journey. The simple wave-rings emanating from the points of origin and end of flight

[1] This genus has almost universally been known of late as *Evolantia* Heller and Snodgrass, 1903. It was based on *Exocoetus micropterus* Valenciennes. But the name *Oxyporhamphus* Gill, 1863, was obviously based on the half-beaked young of the same genus. A comparison of Valenciennes' figure of *Hemiramphus cuspidatus* (Cuvier and Valenciennes, *Histoire naturelle de poissons*, 18 [1846]: 56, Pl. 55), the type species of Gill's genus, with Nichols and Breder's figure (1928) of the beaked young of *Evolantia microptera*, indicates that they are based on the same genus if not the same species. The only discrepancy of moment is in the number of dorsal rays (Valenciennes gives 18 for *cuspidatus* and 15 for *micropterus*). It is possible that the two species are distinct, but more likely that the count for *cuspidatus* is too high. The fact that the two types of *cuspidatus* were taken from the stomach of a bonito might explain a miscount of the rays. Since the generic name *Oxyporhamphus* is older than *Evolantia*, it should replace the latter name.

confirmed my visual impression that none taxied at the surface at the beginning of the flight, and that none attempted a second soar. The flight of the primitive *Oxyporhamphus* is, therefore, much simpler and shorter than that of the more specialized flying fishes, the Cypselurinae.

That the fishes observed really were *Oxyporhamphus* seems certain. I clearly distinguished their slender form, lack of beak, and relatively short pectorals, which are only long enough to reach approximately the rather small pelvic fins. The pectoral fins, though much shorter than those of any other Asiatic flying fish, were much longer proportionately than those of any other surface-swimming Asiatic fish.

III. THE FLIGHT OF THE MONOPLANE FLYING FISHES

The genus *Exocoetus* ("*Halocypselus*" of Jordan and Evermann, and of Nichols and Breder)[2] has also a distinctive type of flight. This the late Charles Henry Gilbert, one of the most acute of fish observers, told me years ago. He related having frequently seen on the high seas of the tropics flocks of this genus making simple leaps of about 10 to 20 meters, a long flight for a fish, though a relatively short one for a typical flying fish (Cypselurinae).

My clearest and surest observations on the flight of *Exocoetus*, made in the Pacific Ocean east and northeast of Luzon (at Lat. 20° to 21° N., Long. 127° to 128° E., surface temperature 28.5° C., and at Lat. 24° N., Long. 128° 30′ E., surface temperature 26.5° C.),[3] confirm these remarks of Dr. Gilbert. Often singly, but frequently in loose to compact groups of about twenty-five, these little flying fishes were there seen to catapult themselves directly out of the water, clearly without undertaking any initial surface-skimming. At times they shot forth at a small angle with the surface, and then their flight did not differ notably from that of the more primitive *Oxyporhamphus*. Often, however,

[2] On the use of this name see Lönnberg, *Bih. Sv. Vet.-Akad. Handl.*, 22 (Afd. 4, No. 1, 1896) : 25.

[3] No flying fishes were identified as *Exocoetus* in the passages among the Philippine Islands, where the Cypselurinae so notably abounded. *Exocoetus* is apparently a fish of the open seas. It has been recorded hundreds of miles from the nearest land.

and probably more typically, they came out at an angle of about 45°, or even more, with the surface. They were then caught by the wind, which when strong wafted them about like pieces of paper,[4] so that at times they were carried 2 to 4 meters above the surface. This high and passive flitting, the lack of initial surface-skimming or taxi movements, the shortness of the flight (not more than 20 meters), and the constant failure to repeat a flight before reëntering the water, all feature the flight of *Exocoetus*,[5] and contrast it strikingly with the low, accurately controlled, long and often compound air movements of the Cypselurinae, in which each flight is induced by a taxi.

The flight of *Exocoetus*, however erratic, like that of *Oxyporhamphus* and the Cypselurinae, is merely a soar. The pectoral fins were clearly seen to be held taut and were neither flapped nor vibrated.

These erratically flying exocoetids were identified as *Exocoetus* because the pelvic fins were not observable. In this genus these fins are small and placed far forward, and are not modified as organs of flight. In the Cypselurinae the pelvics as well as the pectorals are much enlarged, and form conspicuous planes when a fish is soaring. In the large size of the pectoral fins these fishes referred to *Exocoetus* rivaled the Cypselurinae and contrasted strongly with the short-winged *Oxyporhamphus*.

IV. THE FLIGHT OF THE TYPICAL OR BIPLANE FLYING FISHES[6]

In the Cypselurinae, comprising four genera in the classification of Breder (1928), the aërial locomotion of fishes reaches its

[4] The high, flitting flight of fishes of the genus *Exocoetus* doubtless accounts for the circumstance that during storms especially they are often cast upon the decks of large vessels.

[5] Hankin (1920) has indicated a difference in the flight of the "two-winged" and "four-winged" flying fishes which I did not appreciate. He believed that the former lacked the power to check their speed before ending their flight, thus contrasting with the "four-winged" species which he thought slackened their flight by movements of their enlarged pelvic fins just before alighting.

[6] The remarkable analogy of the flight of cypselurine flying fishes to that of airplanes has lately been stressed by a number of authors, most definitely by Breder (1931).

ultimate expression. The manner of flight in these "four-winged" or biplane fishes is not only highly specialized, but appears also to be strikingly uniform throughout this speciose and obviously successful group, which includes all the species of the Exocoetidae, with the exception of *Oxyporhamphus micropterus*, *Exocoetus evolans*, *Exocoetus obtusirostris*, *Fodiator acutus*, and the few species of *Parexocoetus* (Breder, 1928). I have observed in flight the large California flying fish, *Cypselurus californicus*, and at least ten species in the western Pacific, from Java to Japan. In all these I have found the movements in the air to be surprisingly alike. This similarity in flight methods through the group decreases the importance of my inability to distinguish in flight the species observed in Asia.

To illustrate the variety of species of Cypselurinae observed in Asia and to present evidence for their possible future identification, I describe the appearance of some of the forms seen. Most of the notes and records in Celebes Sea on June 3 were based on a very robust species estimated to be 20 to 25 cm. long (over all), with blackish wings. On the next day the same type was observed, but one not quite so robust and with colorless pectorals was perhaps commoner; still another, slenderer and smaller, but distinctly of the biplane type, was flying after the same fashion, though usually in more compact schools (sometimes nearly one hundred would dash out almost simultaneously); rarely, another type, with a wide yellow streak near the outer edge of the otherwise blackish pectoral, was seen on June 4 and subsequently. In the Strait of Basilan, on June 6, most of the flying fishes seen were about 19 to 25 cm. long, without marked color on the pectoral fin. Later that day, out in Sulu Sea, at least four species, mostly larger, 25 to 45 cm. long, were studied, for the coloration of the pectoral fins was of four types: clear, blackish, blackish with a yellow band, yellow. In Bohol Strait, on June 7, the Cypselurinae were mostly 22 to 32 cm. long and fairly robust; the pectorals of some were without noticeable color, but most of them were blackish, and the pelvics of some were also dark. In the Pacific east and northeast of Luzon most of the fishes of the group under consideration were rather large and robust; a few

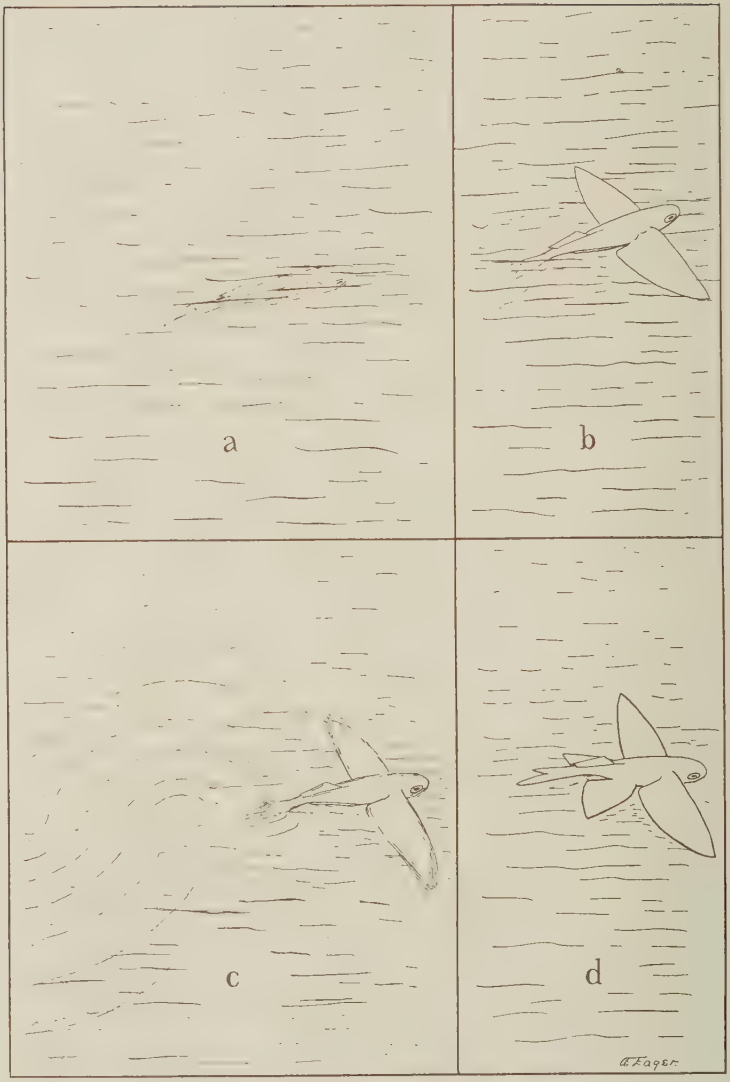

FIG. 66. Four stages in the flight of a cypselurine flying fish (see explanation at bottom of opposite page)

had yellow-brown pectorals (these were seen from just off San Bernardino Strait, where they were rare, and northward in increasing commonness almost to Kyûshû); others were similar, but had clear pectorals. About Japan I observed *Cypselurus agoo* and at least two related species, and also one with black-blotched pectorals.

The cypselurine flying fishes were especially abundant in the passages among the Philippine Islands, where the water was as placid as that of a little lake on a calm day and where the surface temperature varied from 28° to 30° C. They had also been common in the similarly smooth Celebes Sea (32° C.) and Java Sea. They remained rather common in the open ocean east and northeast of Luzon, as long as the temperature remained high (27° to 29°), although they were not so excessively abundant here as among the Philippines. They became scarcer at 24° N. latitude, where the surface temperature was 26.5°, and relatively very few (only 11 seen in three hours) at about 30° N. latitude, where the temperature was 24° to 25° C.

These flying fishes showed a marked tendency to congregate, not only in general regions, but also in schools. At times more than one species would be seen in the air simultaneously, but often whole flocks were clearly of a single species, distinct from another just previously flushed.

The flying fishes swim with great speed in the water, as I long ago saw clearly for *Cypselurus californicus*. I observed that when that species is under water the wings are held tightly against the body (Fig. 66 *a*), and I assume that this fin position must hold true for all the species. On reaching the surface the

EXPLANATION OF FIGURE 66

a. The fish approaches the surface; both pairs of fins folded
b. The fish breaks the surface and spreads the pectoral fins (upper or anterior planes) to support the anterior part of the body
c. The fish gains speed by the taxi or surface-skimming. The caudal beats the water; the body shakes; and the wing tips flutter in response, giving a false illusion of wing beating
d. The fish takes off by spreading the pelvic fins, thus lifting the tail out of the water. The planes are now held taut and rigid as the flying fish dashes through the air

pectorals are at once spread, so quickly indeed that my eye never caught the movement.[7] Since the supporting planes lie well in advance of the center of gravity and since the lower posterior planes, the enlarged pelvic fins, must at first remain folded against the belly, the fore part of the body is held up at a slight angle with the surface of the water, while the elongated and strengthened lower lobe of the caudal fin is partially submerged in the water (Fig. 66 *b*).

The "taxi"

In obtaining this position at the surface of the water there may be some slackening of the speed of the fish. They actually appeared almost to balance themselves for a split second at the inception of the surface movements which are characteristic of this group of flying fishes and which may be termed the "taxi" stage of the flight. At least we may be sure that at the start of the taxi sufficient velocity is not yet attained to carry the fish on a very long soar through the air. That this is true was evident from actual observations. When the taxi was misgoverned, much abbreviated, or even eliminated, on account of some condition of wind, wave, or obstacle, the fish was sustained in the air for only a few feet. And when a very short taxi was employed, the first flight was not much longer.

I believe that I was able to observe the acceleration in speed which I assume is produced by the taxi. In compound flights it was obvious that the slackened speed at the end of one flight was greatly accelerated by the taxi intervening directly between this soar and the following one. At the end of each taxi the fish appears to be catapulted into the air at a very high speed. What this actual speed is would be very interesting to know. I assume that it is not less than about 55 kilometers (35 miles) per hour, my very rough estimate of the average speed of the whole flights (drawn up from guesses of the distance traversed in timed

[7] The folding back of the pectoral fins while the fish swim under water and their spreading only on coming to the surface were observed by Adams (1906, p. 145), who placed some live flying fish in a bathtub on board ship. I suppose that these observations are correct, although this author's account of the actual flight is very peculiar and no doubt erroneous.

flights).[8] That an acceleration takes place during the taxi may also be concluded from the fact that my estimate of the speed of the entire taxi is only 10 meters per second (about 35 kilometers per hour), which is less than my estimate for the whole flight and which is almost certainly less than the speed attained at the end of the taxi and the beginning of the actual flight. The taxi may, therefore, be assumed to accelerate the speed to a degree sufficient to carry the fish for a considerable distance through the air.

The propulsive power by which this acceleration is accomplished is derived solely from a violent side-to-side vibration of the tail, as the fish skims along with only the strengthened lower caudal lobe in the water. The even wave-ring disturbance on the quiet sea surface indicated that such a movement takes place, and the actual track which I once saw left on a dust-covered surface proves the point.

The retention of the propelling organ in the dense medium of water and the supporting of the moving body in the rare medium of air permit the attaining of a very high speed. This is the principle of the speed boat.

The rapid shaking undergone by the stiff body clearly follows from the tail movement. The slight movement of the taut pectoral fins (Fig. 66 *c*) during the taxi has been mistaken by uncritical observers to be an actual flapping of the wings, but this rapid vibration of the fins, like the less obvious but still observable shaking of the whole body, is solely a response to the violent tail movements. The vibration of the wing tips, having an amplitude of only a centimeter or two and usually lasting a bare second, is certainly insufficient to give so heavy a body speed enough to carry it through the air. The hazy outline of the planes becomes transformed into knifelike rigidity, as I have observed hundreds of times for many species and as most other trained observers have indicated, at the instant the tail movements cease when the fish rises into the air.

It is a curious fact that nearly all observers have failed to

[8] This estimate is in rough agreement with those of Hankin (1914, 1920), who computes the air speed of flying fishes to be 10 to 20 meters per second. Hankin estimates the longer flights to be 200 to 400 meters long.

appreciate the simple reason why the wing tips flutter while the tail is vigorously beating the water surface. Even those who have taken the side that flying fishes do not fly by wing-flapping explain this wing vibration as due to the action of the wind on the taut membrane. That this explanation is untrue follows from the fact that the vibration ceases the instant the tail fin leaves the water, although neither the wind pressure nor the wing tautness is then materially lessened.

The distance covered by the initial taxi is quite variable. Very rarely it is entirely omitted by a biplane flying fish (as it normally is by the more primitive *Oxyporhamphus* and by the monoplane *Exocoetus*). The omission is apparently only by accident, as when a fish emerges on the down slope of a sharp wave. The flight is then very short, unless resustained by a taxi as the fish touches the water. Frequently the taxi covers less than 5 meters, in which event the flight is short, though often followed at once by a longer flight induced by a longer second taxi.

The usual taxi distance I estimated, with the aid of a fellow-passenger, Dr. S. Ogawa of the Japanese Hydrographic Office, an expert in navigation, to be from 5 to 15 meters. Some taxis seen were at least 20 meters long. We judged the average to be close to 30 feet (9 meters).

The number of seconds devoted to the taxi, according to fifty-two timings made in Bohol Strait, Philippine Islands, on June 7, when the sea was calm, ranged from almost 0 to 2, with an average of 0.9 second (column two of Table I). The estimate was made by counting the 0.45-second intervals (by ticks of a watch) involved in the taxi. Since the average distance covered by a taxi was judged to be 9 meters, I compute the average speed for the surface period to be 10 meters per second (36 kilometers per hour). This is the speed of an athlete on a short dash. But the speed of the fish, since it is accelerated during the taxi, is probably much higher than 10 meters per second at the end of the taxi, when it hurls itself into the air.

In order to induce this high speed the vibratory motion of the tail must be very strong and rapid. The actual number of vibrations could be roughly counted, by reason of the glasslike smooth-

ness of the surface of Bohol Strait, where the estimates were made. From the vantage point on the navigating deck of the slowly moving steamer, it was found possible to count for about one fourth of the taxi distance the number of rings issuing outward from one side of the path of the fish (each primary ring on each side corresponded to one complete [or double] swish of the tail). For an average taxi (about 9 meters long and of about 0.9-second duration) the number of vibrations was estimated as 40 to 80 (average about 60), and proportionately more or less for long and short taxis. These figures yield average estimates of nearly 70 vibrations per second, and of 7 complete vibrations per meter.

One really accurate estimate of the number of vibrations per meter was made. By remarkably good fortune a flying fish of the subfamily Cypselurinae, about 12 cm. long, rose just beside the ship almost directly below me and made away at right angles, over the glassy Bohol Strait, where the surface happened to be densely covered by a dustlike scum. The track of the fish's tail was left imprinted like a cymograph record on the surface of the sea, as a cleared zigzag trail showing exactly thirty angles on one side. I supposed the distance traversed to be 20 feet (6 meters), and this estimate was confirmed by Dr. Ogawa. This fish, therefore, made five complete (double) beats of its tail on the surface of the water for each meter, a figure regarded as accurate within one beat per meter, plus or minus. This determination is somewhat lower than that based on the average drawn from counts of rings produced by the tail beating (7 per meter), although the two figures are sufficiently close to confirm one another. Judging from the length of this particular taxi as compared with others timed, I estimate this one to have lasted about 0.6 second. As before, this estimate yields an average taxi speed of 10 meters per second and a computed average of 50 vibrations per second.

It appeared from the observations on both the wave-rings and the cleared track, produced by the fish in its taxi movement, that the number of vibrations of the tail per meter did not noticeably increase during the course of the taxi. The distance between

successive rings and the successive points on the zigzag track appeared to be the same at the end of the taxi as at the beginning. A slight and gradual change would probably not have been apparent, but a sharp difference should have been seen under the extremely fortunate conditions of observation. Therefore, since the speed is (presumably) accelerated in the course of the taxi and since the rate of vibrations per meter remains about constant, the number of beats per second presumably increases beyond the average, which was estimated to be nearly 70 per second, proportionately as the speed increases beyond the average for the taxi, estimated at 10 meters per second. Like an airplane, the fish probably increases its power as it approaches its take-off.

On the basis of some field observations (how detailed not indicated) and of aërodynamic computations Shoulejkin (1929) has concluded that a speed of 16 to 18 meters per second is attained at the end of the taxi, and that the average speed during the actual flight is 10 meters per second (covering 100 meters in 10 seconds). Other estimates, as those of Ahlborn (1895) and Hankin (1914, 1920) are in the same order of magnitude as Shoulejkin's and mine.

The subsequent taxis, that is, those which intervene between the successive rises of a compound flight, were seen to be typically shorter than the first (or than the second, if the first start was abortive). They seldom lasted a second, and the average was thought to be about 0.5 second; it may be 0.3 or 0.7 second, but probably lies between those figures. A more accurate estimate could of course be made with special equipment.

A variation in the taxi sometimes occurs in rough weather, when the sharp little troughs of a choppy sea induce short breaks in the surface movement. In general, however, in the taxi as well as in the flight, the cypselurine flying fishes are remarkably adept at holding their course parallel to the changing level of the sea.

The position and function of the fins in flight

During both the initial and intermediate taxiings the pelvic fins must remain folded tightly against the belly, for at these times they were always invisible. But at the instant the fish

leaves the surface these fins flash into clear view and are very easily seen with binoculars or even with the unaided eye, especially when the pelvics are blackish. It is assuredly the upward force of air pressure on these posterior planes that lifts the drooping tail out of the water, and thus actually initiates the air flight proper (Fig. 66 *d*). When the fish is thus forced into a horizontal position, it lies at most only a few centimeters above the sea. This is probably a main reason why many flights are abortive, ending almost at once in a steep little wave. Another example of imperfection in flight sometimes noted was the bare clipping of the crest of a sharp wave by the tail fin, while the fish was volplaning through the air.

The often repeated claims that a flying fish sustains itself in the air by flapping or rapidly vibrating the pectoral "wings" are due, I suppose, to preconceived ideas that fishes must fly like birds, or to uncritical deductions that the mechanics of the situation demand such movement, or to untrained or inattentive observation. These claims have for the most part been made by other than trained naturalists, or by laboratory zoölogists equally untrained in field observation. Such accurate, trained observers as Moseley, Jordan, Gilbert, and many others have been unable to detect any movement of the fish's main planes while it flew through the air. Neither for the California flying fish nor for the several species I studied on the opposite side of the Pacific could I observe any wing movement whatever, which by any reasoning could be thought to sustain the fish in the air. The vibration of the pectoral tips through a small amplitude during the taxi, assuredly the mere consequence of the vigorous sweeping of the tail, as I have already stressed, ceases instantaneously as the caudal fin rises clear of the water. And these fins remain stretched taut and firm until the moment when the fish either dives into the sea, or until its tail fin dips in the water and resumes the violent sculling, which immediately induces a renewal of the hazy appearance of the fin tips. The frequent naïve claims that this secondary vibration becomes apparent only on the fatigue of the fish and that the wing vibration while the fish had been in the air was too rapid to be seen by the eye, are at once negatived

by the fact that the wing appears as a single blade, whereas if it had been moved too fast to follow, it would have appeared double like a humming bird's wing, one image at each end of the stroke.

That there is absolutely no vibration of the outstretched pectoral fins while the fish is in the air is clearly observable, even without the aid of field glasses. Whenever a fish happened to fly directly away from me, therefore under conditions which would make easily evident any up-and-down movement, I always saw the edges of the planes standing out clear like knife edges, without a trace of doubling or of a blur, even when the fish flew into a high wind (which some have said causes a vibration of the fin). It was with full certainty also that I observed the rigidity of the planes hundreds of times as I looked down through field glasses at flying fishes close to the boat. When the pectoral fins were blackish, and better yet, when they were marked with an oblique yellow band or by black blotches, it was especially easy to appreciate that these fins remained motionless in relation to the fish. Such observations from above showed clearly that Adam's claim (1906) of a horizontal vibration of the wings was erroneous.

The anatomical researches of Möbius (1878), Ahlborn (1895), Ridewood (1913), and others have disclosed no muscular or other modification sufficient to make one suspect that these fishes can flap their wings sufficiently to maintain their heavy bodies in the air.

The pelvic fins, the lower or posterior planes, likewise were never seen to vibrate. They remained folded as the caudal beat the surface, and thus did not participate in the slight vibration of the fin tips, induced by this tail movement. Especially when the pelvics were black or blackish it was possible to see through the binoculars that these fins did not vibrate while they were outstretched during the actual air flight.

The fact that the expanded paired fins do not vibrate after the fish leaves the water surface proves that the caudal fin does not beat in the air (another fantasy of some authors). Furthermore, the edge of this fin could be seen clear-cut when a fish volplaned away in line with my vision.

The control of flight direction

I conclude from my observations, therefore, that a flying fish when in the air makes no effort by any flapping or vibration of the fins to add to the velocity it gained by the sculling of the tail during the swimming under water and during the taxi at the surface. That it does, however, use the fins in the air to control the direction of the flight is certain. This control was most often seen when a fish avoided the obstruction of the ship's bow by flying around it in a distinct curve, and even more spectacularly when one headed directly for the ship's side turned off at right angles in a curve with a radius sometimes as short as 3 to 5 meters. When a flying fish approached even closer to the ship, it dived into the water, as I have mentioned for *Cypselurus californicus*, to take advantage of the greater resistance of that medium in making the shorter turn necessary to avoid a collision with the ship. The control is so nearly perfect that I have never seen one strike a vessel, though of course they are known to land on deck at night, and I have found but one published record of a flying fish striking the side of a ship. Occasionally I have seen them collide, not with a ship but with one another (as though to heighten the analogy of their flight to that of airplanes). I suppose, therefore, that flying fishes are lacking either in perfect flight control or in perfect air vision.

In describing the flight of *Cypselurus californicus* I accorded to the lower or posterior planes (the pelvic fins) the function of stabilizing or balancing the fish while in the air.[9] For the generally smaller Asiatic species I was not able with certainty to confirm these observations on the joint or independent movements of the pelvic planes. The tilting of the body and of the pectoral planes up toward a side wind seemed more responsible for a marked deflection of flight in the Asiatic species than did any possible curvature of the tail. I often watched for any definitive movements, especially unilateral ones, of the pectoral fins, but could never observe them. It is true that the angle made by the two

[9] Hankin (1920) has also indicated that the position of the pelvic fins is altered to control the flight, especially to check it.

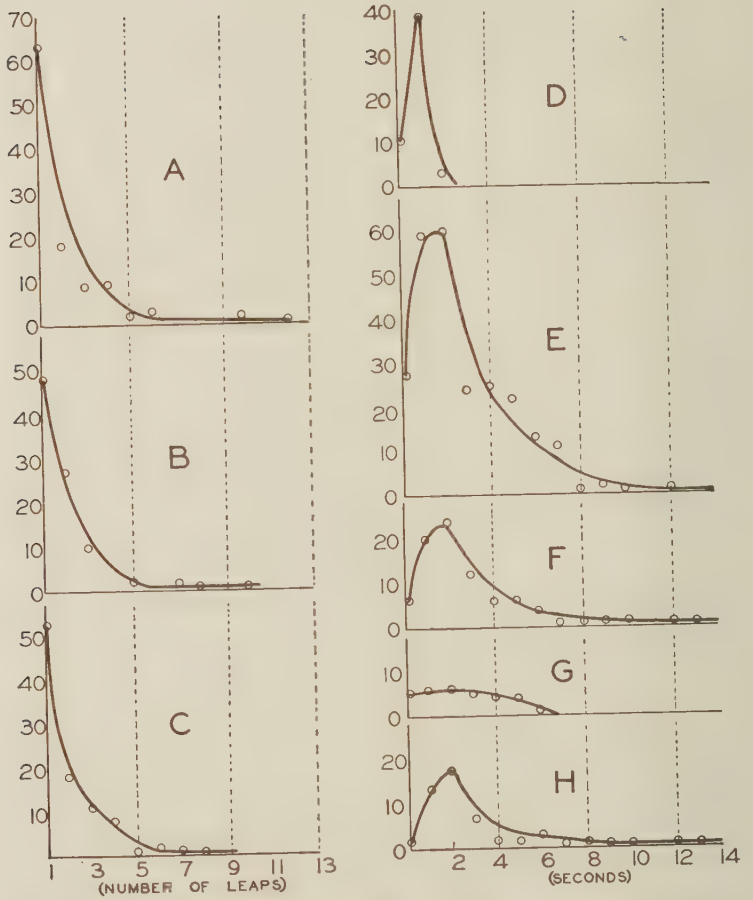

FIG. 67. Statistical analysis of the flight of cypselurine flying fish (see explanation at bottom of opposite page)

main planes, from behind, for example, often varied considerably in either direction from horizontal, but the two fins seemed to be always held at the same angle with the cross axis of the body. This angle I thought varied somewhat between species, and also with degree of fatigue.

The flying fishes of the *Cypselurus* types, like airplanes again, show a vertical as well as a horizontal control of flight direction. This was beautifully evident as they maintained a course nearly parallel with a choppy water surface, just skimming over sharp-peaked crests and dropping to a lower level over the intervening troughs. As already noted, the diving to avoid collision with a ship likewise indicates a vertical control.

The claim has been made that flying fishes invariably take off into the wind, but I have seen them scoot away toward all points of the compass while a strong wind remained in one quarter. The power and speed of the taxi seem sufficient to hurl them into the air, when the pelvic planes are expanded, no matter what may be the angle of the taxi to that of the wind. But after

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EXPLANATION OF FIGURE 67

A–C. Frequencies of number of leaps in each flight, under different conditions

A. Celebes Sea and Strait of Basilan, June 3 and 6, 1929; sea very smooth; usual size of fishes about 19 to 25 cm.

B. Southeastern Sulu Sea, off Mindanao, June 6, 1929; sea slightly choppy; usual size of fishes about 25 to 45 cm.

C. East and northeast of Luzon, in Pacific Ocean, June 8 to 11, 1929; sea rough; usual size of fishes about 25 to 45 cm.

D–H. Frequencies of duration of single flights in seconds

D. Initial taxi: Bohol Strait; sea smooth; moderate wind; usual size of fishes about 22 to 32 cm.; one or more leaps followed the taxi

E. First flight: conditions as for *D*; flight either continued or not

F. First flight: Pacific Ocean, east and northeast of Luzon; sea slightly choppy to very rough; moderate to strong wind; usual size of fishes about 25 to 45 cm.; flight either continued or not

G. First flight: conditions as for *F*; flight continued

H. First flight: conditions as for *F*; flight not continued

the fishes start their flight, especially as they begin to lose momentum, their direction is much modified by a strong wind. They tilt their plane surface more or less upward toward the wind, and are thus carried off their original courses in a wide curve. To what degree the wind is so utilized to prolong or definitely alter the direction of the air journey is a point worthy of detailed inquiry.

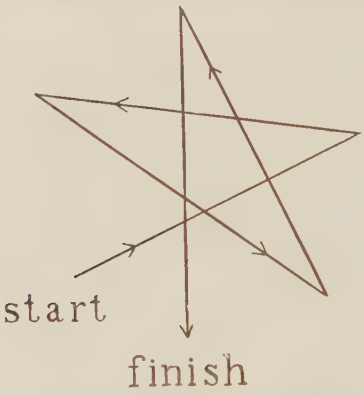

FIG. 68. Diagram of a concentrated zigzag flight, such as is occasionally indulged in by a cypselurine flying fish

Sometimes I saw these fishes make a sharp angle in their flight by barely dipping into the water. When this was repeated several times, with each flight lasting only a half-second or so, a peculiar concentrated zigzag course, such as diagramed in Figure 68, was followed. The fish then acted as though in a fit, but the action may have been wholly normal, perhaps of significance in dodging.

The duration of the flights

During my observations on the species of Cypselurinae in Asiatic waters I made an effort to time a considerable number of flights. Though my estimates have only a moderate degree of accuracy, they are, so far as I know, the most definite which have been made, and suffice at least to show that a person's offhand estimate of the time in the air is usually several times too high. The flights were timed, in the absence of a stop watch, by counting the number of watch ticks (at a calibrated interval of 0.45 second) elapsing during the flight. Altogether 424 flights or parts of flights were timed, 298 in Bohol Strait, Philippine Islands, and 126 in the open Pacific east and northeast of Luzon. The results are tabulated as Table I, and most of them are graphically portrayed as Figures 67 *D–F*.

TABLE I

ESTIMATED LENGTH IN SECONDS OF FLIGHT OF CYPSELURINAE

For the first leap the time is for the actual flight after rising from the surface of the water. For flights of more than one leap the taxi periods (about 0.5 second each) after the first taxi are included. The average time per leap (see next to last row) subsequent to the first flight, which averaged 2.4 seconds, excludes all the taxi periods.

Locality	Bohol Strait, P. I.				Pacific Ocean, east and northeast of Luzon, P. I.						
Date	June 7, 1929				June 8 to 11, 1929						
Sea (and wind)	Smooth (moderate wind)				Slightly choppy to very rough (moderate to strong wind)						
Usual size	22 to 32 cm.				25 to 45 cm.						
Stage of flight	Initial taxi	First flight (not including taxi period)			Total flight (including all except first taxi period)						
Number of leaps	One or more	One or more	One or more	More than one	One only	2	3	4	5	6	7	8
0	10	27	6	5	1	..	..	..	..	..	..	..
1	39	59	20	6	14	2	1	..	..	..	..	..
2	3	60	24	6	18	1	1	..	..	..	..	..
3	..	24	12	5	7	4	1	..	..	1	..	..
4	..	25	6	4	2	2	..	..	..	..	..	..
5	..	22	6	4	2	2	1	..	..	..	..	..
6	..	13	4	1	3	1	..	..	..	..	..	..
7	..	11	1	..	1	2	1	..	..	..	..	..
8	..	1	1	..	1	..	..	1	..	..	1	..
9	..	2	1	..	1	1	2	..	1	..	..	..
10	..	1	1	..	1	1	1	1	..	..	..	..
11	..	..	..	..	..	..	..	1	..	..	..	..
12	..	1	1	..	1	..	..	1	..	..	..	..
13	..	..	1	..	1	2	..	2	..	..	..	..
14	..	..	..	..	..	..	1	..	..	..	..	..
15	..	..	..	..	..	..	..	..	..	..	..	..
16	..	..	..	..	..	..	2	..	..	..	..	..
17	..	..	..	..	..	..	..	..	..	..	..	..
18	..	..	..	..	..	..	..	..	..	..	..	..
19	..	..	..	..	..	..	..	..	..	1	..	..
20	..	..	..	..	..	..	..	..	..	..	..	..
21	..	..	..	..	..	..	..	..	..	..	..	..
22	..	..	..	..	..	..	..	1	..	..	..	..
23	..	..	..	..	..	..	..	..	..	..	..	1
24	..	..	..	..	..	..	..	..	..	..	..	..
25	..	..	..	..	..	..	..	..	..	..	..	..
26	..	..	..	..	..	..	..	..	..	..	..	..
27	..	..	..	..	..	..	..	..	..	..	..	..
28	..	..	..	..	..	..	..	1	..	..	..	..
TOTAL ..	52	246	84	31	53	18	11	8	1	2	1	1
Average per second	0.9	2.7	2.9	2.4	3.2	5.5	8.4	14.4	9?	11?	8?	23?
Average time per leap (excluding taxi periods) ...						2.6	2.5	3.5	1.2	1.2	0.4	2.4?
Weighted average of these average times per leap 2.6												

The longest period any flying fish was timed actually in the air on a single flight was 12 seconds in Bohol Strait (246 timings), and 13 seconds in the Pacific Ocean (84 timings). Some flights which I observed among the Philippines, before I started to use the watch, I believe were somewhat longer than any of those I actually timed. Of 42 compound flights that were timed the longest lasted slightly less than thirty seconds. It is doubtful whether any flights cover a whole minute.

Most flights of the Cypselurinae are short, lasting only one or two seconds, whether the sea be glassy smooth or decidedly rough. The lack of correlation between the time of flights in calm and stormy weather is strikingly shown by the similarity of the graphs portraying my records for Bohol Strait and the Pacific Ocean (Figs. 67 *E*–*F*). The average time for the first flight was about the same, 2.7 seconds for the smooth Bohol Strait, and 2.9 seconds for the rough weather on the open ocean.

The eighty-four observations for the first flight made in the ocean were further analyzed into those for flights at once continued by a subsequent taxi and those ceasing immediately. It appears probable from this analysis (see Figs. 67 *G*–*H*) that incipient or interrupted first flights, and also those which are of moderate duration (2 to 6 seconds), are very often followed by a second flight, but that long initial flights end directly. It is true that definite records are few (31 for continued and 53 for non-continued flights), but the results harmonize with the general impressions gained from a vastly larger number of observations.

The duration of forty-two compound flights, involving two to eight separate leaps, is indicated in the last seven columns of Table I. These records were obtained with the eighty-four discussed in the last paragraph and are directly comparable with them. The average time per leap for compound flights of two to four stages was found to be as high as the average time for the first leap when that initial flight is continued. This follows from the circumstance that the average time for the first flight, which might be expected to be longer than the subsequent flights, is held down by the brief duration of many incipient flights which are continued by a subsequent taxi. The average dura-

tion per leap of flights involving five to eight leaps was shorter, as would be expected, but my figures are too few to demonstrate this expectation conclusively.

The number of successive leaps

In order to obtain some definite data on the frequency and extent of these compound flights which characterize the air movements of the *Cypselurus* type, I made about one hundred counts of the number of successive flights in three different places under as many different conditions. In the Celebes Sea and Strait of Basilan, where the surface was extremely smooth and where flying fishes were rather small (about 19 to 25 cm. long), 107 counts were taken on June 3 and 6. In southeastern Sulu Sea, off Mindanao, where the surface was slightly choppy and the fishes were larger (mostly 25 to 45 cm. long), 97 counts were tabulated on June 6. In the open Pacific Ocean, east and northeast of Luzon, 95 counts were made from June 8 to 11, when the weather was stormy and the fishes were similarly large. The species observed at the three localities were in large part different (see page 583).

The resulting data are assembled as Table II and are graphically set down as Figures 67 *A*–*C*. Slightly more than half of the flights (164 out of 299, or 55 per cent) were not continued at all. About three fourths (76 per cent) ended with either one or two leaps. Nearly nine tenths (86 per cent) of the total ended with one to three leaps, and more than nine tenths (94 per cent) ended with four or fewer stages. Only one flight in 16, on the average, was made up of five or more elements. The greatest number of successive flights observed was 12. It is doubtful whether a greater number is often undertaken.

The similarity in the frequencies of numbers of successive flights under the different conditions of sea, weather, size, and species of fish shows how independent of these conditions is the number of successive flights undertaken. The curves showing the data (Figs. 67 *A*–*C*) are remarkably alike for the three sets. The average number of successive flights of the smaller fishes in the very smooth Celebes Sea and Strait of Basilan is 2.1; of the

TABLE II

NUMBER OF SUCCESSIVE LEAPS IN FLIGHT OF CYPSELURINAE

Locality; date; condition of sea; size of fishes	Number of leaps												Totals	Av.
	1	2	3	4	5	6	7	8	9	10	11	12		
Celebes Sea and Strait of Basilan; June 3 and 6, 1929; sea very smooth; usual size of fishes about 19 to 25 cm..	63	18	9	9	2	3	..	..	..	2	..	1	107	2.1
Southeastern Sulu Sea, off Mindanao; June 6, 1929; sea slightly choppy; usual size of fishes about 25 to 45 cm.....	48	27	10	6	2	..	2	1	..	1	..	..	97	2.0
East and northeast of Luzon, in Pacific Ocean; June 8 to 11, 1929; sea rough; usual size of fishes 25 to 45 cm...	53	18	11	8	1	2	1	1	..	..	..	..	95	2.0
TOTALS.....	164	63	30	23	5	5	3	2	..	3	..	1	299	2.0

larger ones in the slightly choppy Sulu Sea, 2.0; of those, also large, observed during stormy weather on the open ocean, the average is also 2.0.

The return to the water

The flying fishes of the subfamily Cypselurinae finally return [10] to the water in a variety of ways. Sometimes it seems that they just dip below the surface to rise again almost at once, but usually, when once submerged, they do not very soon rise again.

Since the flying fishes usually fly very close to the water, they disappear at the end of the flight so suddenly that it is almost impossible to perceive the fin movements which accompany or cause the end of the flight. Not infrequently one was seen to bend its course rather sharply downward and to dive in so cleanly

[10] Hankin (1920) thought he could distinguish different methods of return to the water by the two-winged and four-winged types. My notes are silent on this point.

as to produce only a slight splash at one spot. I thought that I could see in some such dives a folding of the pectoral fins, which probably happens, for the elimination of these anterior supports and the continual holding out of the posterior planes would certainly produce such a dive. Occasionally one is seen to dive directly into the face of a steep wave, a movement which would require no special manipulation of the planes.

But just as often the alighting is not so neat. The body may strike the water horizontally with a heavy splash, as though both pairs of fins were folded at once. Or the tail may strike first, owing to the fact that the axis often droops during the flight or, perhaps, to the folding first of the pelvic fins. This is the position assumed when a new flight is initiated by a secondary taxi, but unless a violent vibration of the tail is at once begun, the body plows obliquely into the sea so as to raise a distinct wave on either side. At times the return to the water is still more awkward, for the body may so hit it as to be hurled forward or abruptly sideward for a meter or so through the air, to reënter the water with a new splash.

V. THE FUNCTION OF THE WINGS OF YOUNG FLYING FISHES

All of the discussion given thus far, and in the next section, refers to the flight of adult flying fishes, with especial reference to the phyletic development of the flight. It is of high interest also to study the ontogeny of flight in the same fishes.

In very young flying fishes, to a length of about 1 to 2 cm., the paired fins have not yet become greatly enlarged. This phenomenon has been discussed by Derjugin (1908) and observed by many others, including myself. Between the lengths of about 1 and 2, or of 2 and 3 cm., depending on the species, the pectoral and pelvic fins grow disproportionately fast, to attain a relatively huge size.

During this stage of fin development the baby exocoetids live near the surface, especially about floating *Sargassum* and trash. In this habitat at Hamada, on the Sea of Japan, in a quiet cove called Matsubara Bay, I found, in late July, many young 1 to 5 cm. long. Here they were concentrated in abundance, for the

floating material swept in by the Tsushima branch of the Kuro Shiwo accumulated in the cove. The young of at least three species of *Cypselurus* were represented.

The smallest exocoetids were seen slowly wriggling their way through the water. The smaller ones with enlarged fins, 2 to 5 cm. long, whenever undisturbed, were seen quietly floating near the surface of the water with their enormous, almost circular, paired fins widely expanded. In the species having the paired fins blackish, and in the one having these appendages black-blotched, the quiet extension of the fins was observable from the skiff with certainty. I conclude that the widespread fins of these young flying fishes 2 to 5 cm. long function as flotation organs.

These fins of young exocoetids seem proportionately as large in area as in the adult. The pelvics are especially immense. The pectorals, though shorter relatively than in the adult, are wider because of the more expanded interradial membranes. They resemble the corresponding fins of the "flying" gurnard. The similarity was enhanced by the flexibility of the fin, which in each species appeared sufficient to support the body in dense water but not in rare air.

The smaller of the young exocoetids observed, 1 to 3 cm. long, made only feeble, sluggish efforts to escape, with but little folding of the wings. Somewhat larger ones, however, swam off more quickly, with their great planes folded back out of the way, as they probably also are during all the underwater movements of the adults. But even these young did not attempt to fly in their rush to escape. It is apparently only after a length of about 5 cm. has been reached that the young flying fishes (of the cypselurine species observed) have attained enough strength, and stiff enough planes, to make flight possible.[11]

The first flights are, of course, short. In Matsubara Bay, young 5 to 8 cm. long were frequently seen at very close range

[11] Breder (1932) asserts that young of *Parexocoetus* larger than 10 mm. are capable of air "glides" amounting in the larger ones to at least a foot. This is surprising, since at this age the pectorals are limp. These fins may help to sustain the fish in the air, on account of its very light weight.

to make single, simple leaps of 1 to 10 meters. Neither here nor in Bohol Strait, Philippine Islands, where I observed many young taking to the air on June 7, nor elsewhere, did I see a young flying fish taxi before its flight. It seems improbable that none of these young were members of the Cypselurinae, the only speciose group in the family, all of which as adults initiate their flight with a taxi. Some of those I saw in the air at Matsubara Bay seemed to belong to a species with characteristic black blotches on the pectorals; of these I took many young 2 to 5 cm. long. It is possible that I overlooked a short initial taxi, although I saw many leave the water within a few meters of my position at the bow of a skiff. If the young of the *Cypselurus* group merely leap out of the water after the fashion of the primitive flying fish *Oxyporhamphus* (*Evolantia*), they may be exhibiting a recapitulation in flight evolution. That interpretation is contradictory to the evidence for the independent origin of flight in *Oxyporhamphus* and the *Cypselurinae* (see p. 605).

Having fresh in my mind the strange claim of Nichols and Breder (1928*a*, p. 66) that young flying fishes, unlike the adults, buzz their wings like an insect, I looked sharply for any such movement wherever I saw the young taking to the air. Although the conditions for observing the early flights were almost ideal at Matsubara Bay, here as elsewhere I failed to obtain any visual indication whatever that the wings of young exocoetids are vibrated. And Breder himself has now stated (1929*a*, p. 281), as a result of his recent studies of flight of fishes at Tortugas, "that absolutely nothing was suggested by either experimental or observational methods that would lend any support to the idea that there may be some *functional* wing motion. This holds for the smallest which are just able to clear the water to the largest adults seen."

VI. THE EVOLUTION OF FLIGHT IN THE EXOCOETIDAE

The fact that I observed the flight of the most primitive of the true flying fishes prompts me to discuss briefly the evolution of flight in this family. Sustained flight of fishes might well be assumed to have had its origin in simple air leaping, practiced

by many fishes. In the similar types of leaps the fish merely launches itself into the air, to fall back with a splash near the point where it left its element. The leaping tuna, *Thunnus*, which I observed in abundance in Basilan Strait of the Philippine Islands, does better, sometimes rising several feet above the surface. The striped mullet, *Mugil*, which I watched in California, Java, and Japan, and the fresh-water atherine *Labidesthes*, which I have studied in Michigan (Hubbs, 1921), leap out of the water for distances as much as ten to twenty times their own length. They progress through the air in a low arc, and usually reënter the water in a dive. *Mugil* and *Labidesthes*, both Percesoces, have rather well developed, stiff pectoral fins, which they presumably spread to help maintain themselves in the air.[12] In any event their leaping may be regarded as an approach toward flight.

Probably some of the Synentognathi, to which the Exocoetidae belong, exhibit a lesser approach toward flight than do *Mugil* and *Labidesthes*. The weak little species of *Hyporhamphus*, like *H. rosae* of California, probably seldom take to the air. I have never seen them do so, nor has Barbour (1918), who has attributed to a belonid the surface-skipping of a hemiramphid noted by Nichols (1917). Breder informs me, however, that *Hemiramphus brasiliensis* does skitter along the surface. Somewhat stronger species of half-beaks, as *Hyporhamphus sajori* of Japan, are capable of leaping out of the water about as far and as well as do *Mugil* and *Labidesthes* (I observed this species leaping in Mutsu Bay, northern Japan). The large, bandlike hemiramphid with considerably enlarged pectoral fins, *Euleptorhamphus*, Breder informs me, attempts to skitter along the surface, but falls over on its side and skips for a short distance like a flat stone. Since that genus is highly specialized in a direction away from the Exocoetidae, any proficiency in air locomotion it may have was doubtless derived independently of the flight of the flying fishes proper.

A considerable variation in power of air movement presumably

[12] Breder informs me that he has definitely observed the pectorals of *Mugil* (and of *Hemiramphus*) spread while the fish is in the air.

also characterizes the Belonidae or sea gars, a family of Synentognathi probably less akin to the Exocoetidae then are the half-beaks. The smaller, weaker species without a strongly forked caudal fin (*Strongylura*) must have no great ability in the air, for such movements have not been emphasized in the literature, and I have not seen them. The stronger belonids, of the group called *Tylosurus*, are known to rush forward just out of the water, after the fashion of a hydroplane. They are thus propelled for many meters by a violent vibration of their caudal fins, the strengthened lower lobe of which remains in the dense medium of the water. I have myself seen, and others have reported to me having seen, a large East Indian species of *Tylosurus* engaged in such surface-swimming. Barbour (1918) has observed West Indian species rushing along the surface for as much as two hundred yards, occasionally skipping clear of the water.

This surface, hydroplane-like skimming of *Tylosurus* fails to initiate an actual flight, because this fish cannot spread its "wings" widely enough to support the body in the air for more than short skips. The surface rush of *Tylosurus* corresponds with the taxi stage in the flight of the Cypselurinae, but is, I assume, of independent origin, because the weaker and probably more primitive belonids presumably have no such power of air movement and because the most primitive flying fishes also lack such surface locomotion.

We thus find considerable evidence of convergent or parallel evolution of air movements in the Synentognathi, which are all surface fishes and which, as such, might be expected to tend to take to the air. The differences in the type of flight in different exocoetids leads me to wonder whether the flight of the true flying fishes was really evolved monophyletically. The mere leaping of *Oxyporhamphus* and *Exocoetus* was of course derived from the leaping habits of more primitive fishes. The longer flights of *Cypselurus*, induced by surface-skimming or taxi movements, may well have been derived from some ancestor which had developed such surface-skimming, much as *Tylosurus* has.

A number of authors, taking cognizance of the very good evidence that the Hemiramphidae are ancestral to the Exocoeti-

dae, have made an effort to align the genera of the two groups into a single phyletic series. The most elaborate discussion, by Schlesinger (1909), involves the series *Hemiramphus* → *Euleptorhamphus* → *Oxyporhamphus* → *Hemiexocoetus* → *Exocoetus*. The true relations are not so simple. As stated above, *Euleptorhamphus* is strongly modified into its own peculiar form, which is ribbon-like, and it cannot stand in the direct series leading to the terete flying fishes. *Hemiexocoetus*, as Breder (1928) has proved and as I appreciated in 1916, is merely the beaked young of the flying fish *Fodiator*. And *Oxyporhamphus*, it now becomes apparent, is the beaked young of the genus later called *Evolantia*. The significance of the retention of the half-beak character by the young of the most primitive genus in what appear to be the two lines of evolution in the Exocoetidae has been duly stressed in the papers by Nichols and Breder.

Whatever may be the evolutionary history involved, notable differences mark the flying ability of various flying fishes. The most primitive and most *Hemiramphus*-like exocoetid, *Oxyporhamphus* [*Evolantia*] *micropterus*, merely leaps through the air, maintaining a short, direct, low flight because of the considerable support given by the spread pectoral fins, which, though very small for a flying fish, are much larger than those in most fishes (see p. 580). The oceanic monoplane flying fishes, *Exocoetus* proper (*Halocypselus* of some authors), which, according to Nichols and Breder (1928*a*, 1928*b*), belong to the same evolutionary branch as *Oxyporhamphus*, also shoot directly out of the water. Their much larger pectorals, however, sustain them for longer, higher, and more irregular flights. Their pelvic fins are not properly modified for the accurate control of their flight, which is specialized in the direction of the erratic. These fishes tend to shoot upward where air currents waft them about.

The flight of the four-winged or biplane flying fishes, Cypselurinae, is so different from that of *Oxyporhamphus* and *Exocoetus* as to suggest the possibility of a distinct origin. Unfortunately, there is no description of the flight of *Fodiator*, the genus which links the Hemiramphidae with the Cypselurinae, just as *Oxyporhamphus* (*Evolantia*) may be taken as a connecting link between

the Hemiramphidae and *Exocoetus* (Nichols and Breder, 1928*a*, 1928*b*). I venture to predict that *Fodiator* will be found to have strong surface-skimming powers, but only limited ability in actual flight. *Parexocoetus*, which connects *Fodiator* with *Cypselurus* and its allies, has definitely been observed by Breder to initiate rather well developed flights by surface-skimming. In his published account Breder (1929*b*, p. 309) made the identification somewhat tentatively ("supposedly *Parexocoetus*"), but now informs me, by letter: "Since then I have confirmed this observation at the Dry Tortugas and on two trips to the Bahamas. Just recently in the Tongue of the Ocean I saw these fishes doing this sort of thing [taxi]. It is usually of short duration, and essentially as pointed out in the reference given above." We therefore have some evidence to indicate that the flight of the Cypselurinae and its precursors originated in surface-skimming, whereas that of *Oxyporhamphus* (*Evolantia*) and *Exocoetus* developed independently from the leap.

That the surface-skimming should have been introduced in the evolution of flight after the specialization of the leap seems improbable, though of course not impossible. But the fact that young flying fishes probably belonging to the Cypselurinae, which initiate their flight with a taxi, apparently leap directly out of the water (see p. 603), may be taken as contrary evidence. These little fishes may have been recapitulating an *Oxyporhamphus* stage of flight. A more extended and detailed systematic study of the entire family Exocoetidae should yield new evidence on the possible independent origin of *Oxyporhamphus* and *Exocoetus* on the one hand, and of *Fodiator*, *Parexocoetus* and the Cypselurinae on the other.

The flight of *Cypselurus* is characterized not only by the initial surface-skimming or taxi, but also by its great length and accurate control. It is the consummate in flight of fishes, probably the limit in soaring flight obtainable by so heavy a body supported by a wing limited in size so as not to interfere with the underwater movements of the caudal fin. These four-winged flying fishes are the masters of both water and air, submarines and airplanes in one.

VII. SUMMARY

These field studies on the flight of fishes were made in eastern Asia, in 1929, under very favorable conditions. Only members of the Exocoetidae were seen in flight. The flying of the so-called flying gurnard is held to be a myth. The pectoral fins of *Dactylopterus* could not support the body in the air. As to the so-called fresh-water flying fishes, evidence is considered good for flight in the Gasteropelecinae of South America, whereas there seems to be no sound basis for thinking that the African *Pantodon* flies. There is no good evidence that any fishes fly, except those belonging to the marine Exocoetidae and the fresh-water Gasteropelecinae.

The flight of the most primitive flying fish, *Oxyporhamphus* [*Evolantia*] *micropterus*, is described for the first time. It consists of a low, single leap of about 5 to 8 meters. The genus *Exocoetus* also emerges directly from the water, but typically at a greater angle, so that it rises farther above the water and is wafted about by high winds. The similarity in flight of these two genera confirms the view that they are related.

In the Cypselurinae flight of fishes reaches its ultimate perfection; the success of the group is indicated by its abundance of individuals and of species. In this group flight is initiated by the surface-skimming or taxi movements.

The taxi averages about 9 meters in length. During it the fish moves about 10 meters per second and vibrates its tail 5 to 7 times per meter, or nearly 70 times per second. Toward the end of the taxi the speed of movement and of vibration is doubtless accelerated beyond the average. The sole propulsive power is the side-to-side sweeping of the caudal fin. The retention of the caudal in dense water while the body is held and moved through the rarer medium of air permits the attaining of the high speed necessary to drive the fish on its long glide through the air.

While a fish is actually in the air, there is no further acquisition of power, except such as may be derived from favorable utilization of air currents. There is a slight insignificant vibration of the wing tips during the taxi, a mere shaking induced by

the violent sweeping of the tail, but the wings are stretched taut during the flight. The fish rises from the taxi by the spreading of the pelvic fins or posterior planes, which elevates the posterior part of the body. By fin movements the cypselurine controls its flight with a high degree of accuracy both horizontally and vertically.

The duration of flight was determined by the timing of 424 flights or parts of flight. The longest single flights were of 12 and 13 seconds; the longest compound flight, almost 30 seconds. Most flights last only 1 or 2 seconds; the average, 2.8 seconds. The duration of flight, in my observations, was independent of smoothness or roughness of sea, or of size or species of fishes (within the Cypselurinae).

Successive flights, each induced by a new taxi, are characteristic of the Cypselurinae. About one hundred counts were made under each of three different conditions (smoothness of sea and size and species of fish). The results were surprisingly uniform. Slightly more than half of the flights were not continued; 94 per cent ended in one to four leaps; the greatest number of elements observed in a compound flight was 12; the average, 2.0.

The methods of returning to the water are various.

Very young flying fishes (up to 1 or 2 cm.) have small fins and wriggle through the water. As the fishes grow from 1 to 2, or from 2 to 3 cm., the paired fins become enormously enlarged. They first serve as flotation organs, for the fishes are too weak and the fins are too flexible and too much expanded sidewise for flight. The first flights are apparently short leaps. In these glides, as in the air movements of the adults, there is no apparent beating of the wings.

Many fishes make leaps of varying length and perfection. Certain of the Percesoces are adept at leaping. Some of the relatives of the flying fishes leap; others only skim the surface. These two types of aërial locomotion were probably independently evolved. Since some flying fishes merely leap, whereas others initiate their flight with surface-skimming or taxi, doubt is thrown on the monophyletic origin of flight in the true flying fishes.

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THE INCREASED GROWTH, PREDOMINANT MALENESS, AND APPARENT INFERTILITY OF HYBRID SUNFISHES*

CARL L. HUBBS AND LAURA C. HUBBS

THIS is the third report on our investigation of interspecific hybridization in the sunfishes (Centrarchidae). The data included on the increased growth rate of the hybrids confirm and extend the results presented in the first paper (Hubbs and Hubbs, 1931). The sections on the sex ratio and the infertility of the hybrids are sequels to the second paper (1932).

We are indebted to a number of colleagues and students who have aided us in collecting and studying hybrid fishes, in maintaining our aquarium stock, and in preparing the reports. Samuel N. Jones cared for the live fish; Chester A. Lawson made the sex-ratio determinations, and he and Professor Harry W. Hann prepared slides of sunfish testes; Doctors Carl V. Weller and John C. Bugher prepared the photomicrographs from several of these slides, and assisted in their study. Others, too, have helped. A grant from the Faculty Research Fund of the University of Michigan has made it possible for us to crowd these investigations into an already overfull program.

I. Increased Growth of the Hybrids

Apomotis cyanellus × *Helioperca incisor*

As mentioned in our second paper (1932, p. 436), the laboratory-reared sunfish of this combination [1] "also showed a very rapid growth rate. The 31 remaining offspring of the first mating

* Contribution from the Museum of Zoölogy and from the Institute for Fisheries Research, University of Michigan.

[1] By inadvertence the combination was stated as *Apomotis* × *Eupomotis* in presenting the figures here repeated.

when one year old varied from 46 to 96 mm. long to caudal (average, 64.6 mm.), and the 30 offspring of the second mating at the age of one year varied from 48 to 119 mm. (average, 69.5 mm.)." This rapid growth continued, especially in those not subjected to poor conditions while being held over in a small pond during their second summer. These same fish were overcrowded on being brought back into the aquarium, and hence have not enjoyed good growth conditions. Some of the individuals attained a remarkably large size at the age of 22 months. At that age the 41 remaining fish of both broods varied in size as indicated in Table I.

TABLE I

SIZE OF LABORATORY-BRED AND -REARED HYBRIDS, *APOMOTIS CYANELLUS* × *HELIOPERCA INCISOR*, AT THE AGE OF 22 MONTHS

Lengths measured to caudal fin, to nearest 5 mm.

Size	Specimens	Size	Specimens	Size	Specimens
50	1	90	1	130	2
55	..	95	3	135	2
60	6	100	2	140	..
65	3	105	1	145	1
70	2	110	2	150	1
75	2	115	1	155	1
80	3	120	2	160	..
85	3	125	..	165	2

Average size, 96.5 mm.

Two of these twenty-two-month-old hybrids were actually more than 8 inches long over all. Such a size would ordinarily be considered all but impossible for sunfish so young.

Apomotis cyanellus × *Eupomotis gibbosus*

Of either reciprocal cross of this combination referred to in our second paper too few have survived to give a reliable estimate of average size and growth. It is of interest to note, however, that the largest one of the cross *Apomotis* ♂ × *Eupomotis* ♀ had attained at the age of just 9 months a length of 99 mm. to caudal,[1] and was then engaged in nest building. This is the most precocious example of breeding activity which we have

[1] At 16 months of age this fish was 122 mm. long.

ever observed or heard of, for any sunfish. Several of the larger offspring of the cross *Eupomotis* ♂ × *Apomotis* ♀ entered into territory-holding and nest-building performances when just a year old.

We have two additional sets of data (Tables II–III) on the relative size of nature-reared hybrids of this combination and their parent species. The first set (Table II) is based on two

TABLE II

Comparison of Size of Hybrid Sunfish, *Apomotis cyanellus* × *Eupomotis gibbosus*, with That of the Parent Species
Willow Run collection of November 31, 1931, and January 20, 1932

Size group, in mm.	Year group I *			Year group II *		
	Apomotis	Hybrids	*Eupomotis*	*Apomotis*	Hybrids	*Eupomotis*
22–25	2	1	11	..	..	..
26–29	5	5	40	..	..	..
30–33	6	6	64	..	..	..
34–37	3	10	44	..	..	..
38–41	2	15	34	..	..	..
42–45	2	3	21	..	..	..
46–49	..	4	15	..	..	2
50–53	..	..	8	..	..	7
54–57	..	..	4	..	..	4
58–61	..	..	1	..	2	6
62–65	..	..	..	..	..	5
66–69	..	..	..	..	3	2
70–73	..	..	..	..	..	2
74–77	..	..	..	1	1	1
78–81	..	..	..	..	1	2
82–85	..	..	..	..	1	1
Total	20	44	242	1	8	32
Av.(M)	32.5	36.8	35.5	75 (?)	70.0	60.9
PE_M	.88	.60	.32	..	2.09	1.13
$\frac{\Delta_M}{PE_{\Delta_M}}$		4.0	1.9			3.8

* Age was determined by examination of scales of all specimens, except most of those less than 40 mm. long.

winter collections made at the mouth of Willow Run, near Ypsilanti, Michigan. This is the stream which, where dammed, forms Wiard's Pond, from which we obtain the first series of natural hybrids showing increased growth rate (see 1931 paper). The hybrids in this new series also average larger than the parent species, although the differences, if they stood alone, would not suffice to demonstrate with certainty the increased growth rate of the hybrids.

The second of the new sets of data (Table III) indicating that the *Apomotis* × *Eupomotis* hybrids grow faster than either parent species is based on a collection from Middle River Rouge, by the federal hatchery at Northville. Here the hybrids of this combination have for the last few years at least outnumbered both parent species, obviously as a result of differential upstream migration from Phoenix Pond some distance below (this greater tendency of the hybrids to stem the rather swift current of the stream is probably, like their greater growth, a manifestation of hybrid vigor). The increased growth of the hybrids is significantly indicated by this collection.

Eupomotis gibbosus × *Helioperca incisor*

For the hybrid between the pumpkinseed and the bluegill we now have the most conclusive evidence for hybrid vigor in the growth rate. Although we have still been unable to verify this hybrid combination by an experimental mating, we feel fully confident of our interpretation of certain sunfish caught in nature as of this combination. The very aberrant sex ratio which they show and the abnormal germ-cell structure indicated appeal to us as sufficient confirmation of the systematic and ecological evidence of their hybrid nature.[2]

The large collection of young and yearling sunfish used in this analysis was a random sample taken from the catch of a

[2] Since this was written Dr. David H. Thompson of the Illinois State Laboratory of Natural History has informed us that one of his staff, Dr. Wilbur M. Luce, has successfully crossed *Eupomotis gibbosus* and *Helioperca incisor*, by means of artificial fertilization, and kindly allows us to announce this result.

TABLE III

COMPARISON OF SIZE OF HYBRID SUNFISH, *APOMOTIS CYANELLUS* × *EUPOMOTIS GIBBOSUS*, WITH THAT OF THE PARENT SPECIES

Middle River Rouge collection of August 28, 1932

Size group, in mm.	Year group I *			Year group II *			Year group III *		
	Apomotis	Hybrids	*Eupomotis*	*Apomotis*	Hybrids	*Eupomotis*	*Apomotis*	Hybrids	*Eupomotis*
53–57	..	..	1	..	..	..	..	..	..
58–62	1	..	4	1	..	..	..	..	..
63–67	..	6	4	6	..	..	..	..	..
68–72	..	16	3	5	..	..	..	..	..
73–77	..	17	..	6	..	1	..	..	..
78–82	..	11	..	6	2	1	..	..	..
83–87	..	4	..	2	6	4	..	..	..
88–92	..	1	..	2	7	1	..	..	6
93–97	..	..	..	..	4	1	..	..	1
98–102	..	..	..	..	1	..	..	1	..
103–107	..	..	..	1	3	..	..	..	1
108–112	..	..	..	..	4	..	..	2	..
113–117	..	..	..	..	..	..	..	1	1
118–122	..	..	..	..	..	..	..	..	..
123–127	..	..	..	..	..	..	..	..	..
128–132	..	..	..	..	..	..	..	1	..
Total	1	55	12	29	27	8	..	5	9
Av.(M)	60.0	74.5	63.8	75.3	93.7	85.0	..	113.0	95.0
PE_M	..	.54	.94	1.2	1.3	1.4	..	3.3	2.0
$\frac{\Delta_M}{PE_{\Delta_M}}$			9.9		10.4	4.6			4.7

* Age was determined by examination of scales of all specimens.

single seine haul in Crystal Lake, Oceana County, on October 25, 1931. They were thus near the end of the year's growth. Despite the crowding (6,491 fish were seined about one small brush shelter) they showed full stomachs and a good growth for 1931. Fortunately for the hybrid growth studies, the sunfish in this lake had grown much less rapidly in 1930 than in 1931. Consequently, by making use of scale studies and of growth computa-

tions, we obtained from this one collection four comparisons of the growth of the hybrids and their parent species, namely:

1. During their first year of growth in a poor growing season (1930);
2. During their first year of growth, in a good growing season (1931);
3. During their second year of growth, in a good growing season (1931);
4. Over two years of growth, the first poor, the second good.

The poorness of the first year's growth of the fish taken as yearlings in 1931 is strikingly shown in their scale structure (Pl. LXIV). The winter mark, which was the scale margin at the end of the first year's growth, is ordinarily far in toward the focus of the scale. Of 472 specimens, representing hybrids and both species, none showed a scale which at the first winter was half as long as it had become by October 25 of the second year of life. This indicates a consistently smaller growth in 1930 than in 1931.

To obtain an accurate computation of the size which the yearling fish of 1931 had attained at the end of their 1930 growth, it was found necessary to make a correction in the computation formula ordinarily used. By applying the simple formula, computations of size at the end of the first winter for some of the pumpkinseeds were as low as 10 mm., yet the scales showed that these fish had made considerable growth before their first winter. A size of 10 mm. at that time is an absurdity, for sunfish of that size are still postlarval, and the scales do not appear until a length of about 15 mm. has been attained. By the use of the uncorrected formula, which assumes a simple direct proportion between scale growth and fish growth, computations of size at the first winter have often been found to be too small. This was true for our previous computations for the growth of sunfish in Wiard's Pond. Using two-year-old fish taken in the winter of 1929 30, we computed the average size at the end of the first season's growth (1928) to be 22.6 mm.; but we had determined the average growth to be 27.9 mm., by measuring the fish of the same year class in the winter of 1928–29 (see Table IV).

Creaser's (1926) study of the relation of scale growth to fish growth in the pumpkinseed indicates what correction needs to be made in the formula. For the first two years of life he found

the relation of growth of either the anterior field alone or the whole scale, to the growth of the fish, to be expressed approximately by a straight line. The simple formula would hold only if this straight line when extended would pass through the 0–0 point on the graph. The line, however, for either anterior field or whole scale, intercepts the abscissa at a point corresponding to a fish length of 12 mm. According to the principles of analytical geometry, this is the value to use in correcting the formula, without regard to the size of the fish when the scales were first formed (about 15 mm.). These two values do not agree, because the scale is first laid down as a focus, then grows very rapidly until the scales attain the normal degree of imbrication. Consequently, the formula for growth computation in the pumpkinseed sunfish (valid only during the first two years of life) is:

$$\left.\begin{matrix}\text{Computed length in mm.}\\ \text{at end of first year}\end{matrix}\right\} = 12 + \frac{\text{Scale measurement to first winter mark}}{\text{Measurement of scale to margin}} \times \left\{\begin{matrix}\text{(Actual size of fish}\\ \text{in mm. } - 12)\end{matrix}\right.$$

Applying this formula to our Wiard's Pond data, we obtain computations agreeing very closely with the measured values and thus confirm the validity of the formula as corrected (see Table IV).

TABLE IV

First Season's Growth of Pumpkinseeds in Wiard's Pond in 1928, as Measured and as Computed by the Corrected and Uncorrected Growth-Computation Formulas

	Size groups in mm.							Total	Average
	13–16	17–20	21–24	25–28	29–32	33–36	37–40		
Actual measurements of fish	..	8	53	162	137	29	4	393	27.9
Computations by corrected formula	..	..	20	48	50	14	1	133	28.4
Computations by uncorrected formula	13	29	45	35	10	1	..	133	22.6

Since Creaser's work (see his Fig. 7) showed an especially even relation between growth of whole scale and of fish over the first two growing seasons, we measured the whole scale length (and the longer diameter of the first annulus) on our Crystal Lake sunfish. In the lack of any good data on the relation of scale growth to fish growth in the hybrids or the bluegills, we have had to assume that the same relation holds for these as for the pump-

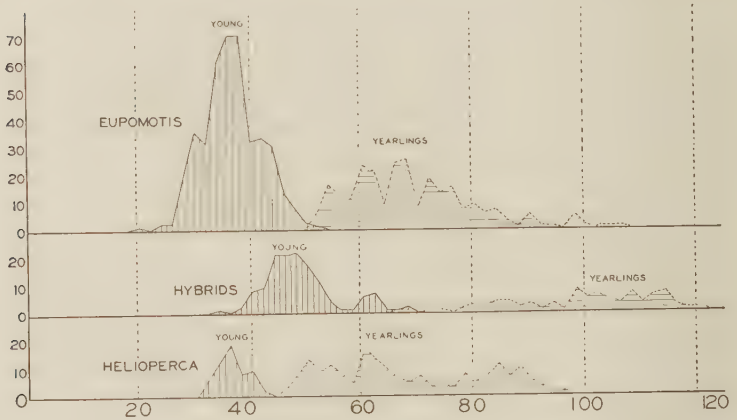

Fig. 69. Measured size frequency distribution of young and yearling hybrid sunfish, *Eupomotis gibbosus* × *Helioperca incisor*, and of parent species, from Crystal Lake, Michigan, October 25, 1931. Lengths in millimeters plotted as abscissae; number of individuals as ordinates. The class interval is 2 mm.

kinseeds. This assumption is no doubt sufficiently accurate for our present purposes.

The results of the computed and the measured growth of the hybrids and of the pumpkinseeds and bluegills in the Crystal Lake collection are shown in Table V and in Figures 69–70. All four sets of comparisons, covering first and second years of growth and total growth, the first year in a bad and in a good season of growth, show consistently and significantly that *the hybrids grew faster than either parent species.* The differences between the

mean values, and the number of times these differences exceed the probable error of the differences, are indicated in Table VI.

Since we have found that hybrids are usually males and that the males in all sets seemed to grow somewhat faster than the

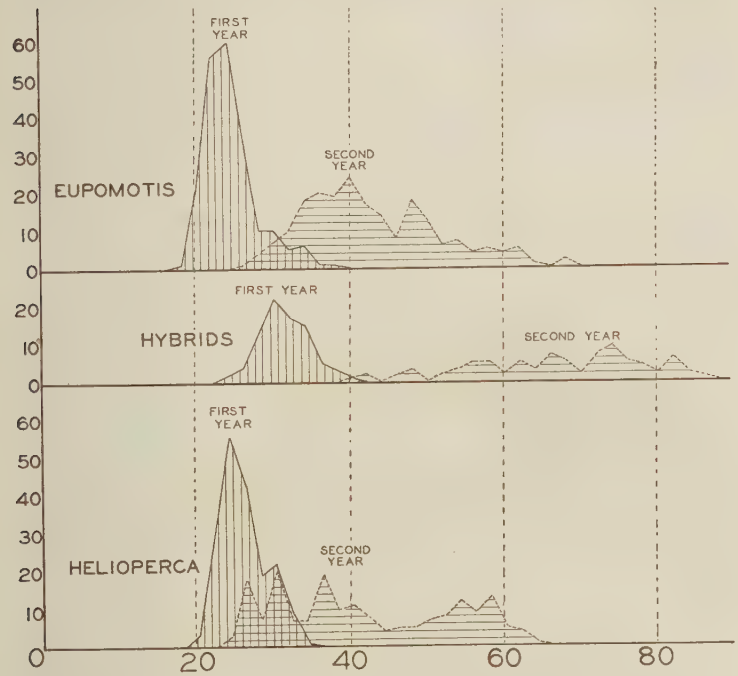

FIG. 70. Computed growth of hybrid sunfish, *Eupomotis* × *Helioperca*, and of parent species, from Crystal Lake, Michigan, for the entire first year and for the second year till October 25. The method of computation is detailed in the text

females in their second year of life, the increased size of the yearling hybrids might be thought to be due to their predominant maleness. This explanation could not apply to any observed differential growth in the first year, when no significant sexual variation in size is evident. That it accounts for only a small

TABLE V

COMPARISON OF SIZE AND GROWTH OF HYBRID SUNFISH, *EUPOMOTIS GIBBOSUS* × *HELIOPERCA INCISOR*, WITH THAT OF PARENT SPECIES

Crystal Lake collection of October 25, 1931

Size group mm.	Computed growth						Measured size					
	First year (1930)			Second year (1931)			Young of year*			Yearlings*		
	Eup.	Hyb.	*Hel.*	*Eup.*	Hyb.	*Hel.*	*Eup.*	Hyb.	*Hel.*	*Eup.*	Hyb.	*Hel.*
18–21	23	..	4	..	..	..	1	..	..	..	..	..
22–25	116	2	85	..	..	3	2	..	..	..	..	..
26–29	44	18	62	5	..	25	20	..	..	..	..	..
30–33	15	39	31	17	..	27	66	..	6	..	..	..
34–37	7	20	1	38	..	26	130	1	31	..	..	..
38–41	1	4	..	43	1	21	102	10	17	..	..	..
42–45	...	..	..	30	2	12	63	30	2	..	..	..
46–49	...	..	..	26	5	10	21	43	..	..	..	11
50–53	...	..	..	19	2	15	3	28	..	22	..	22
54–57	...	..	..	11	8	21	...	5	..	23	..	19
58–61	...	..	..	9	7	18	...	7	..	44	..	22
62–65	...	..	..	6	8	5	...	8	..	33	..	23
66–69	...	..	..	2	12	..	...	3	..	33	2	10
70–73	...	..	..	..	9	..	...	..	..	31	1	10
74–77	...	..	..	..	14	..	...	..	..	22	1	7
78–81	...	..	..	..	6	..	...	..	..	15	5	13
82–85	...	..	..	..	8	..	...	..	..	10	7	18
86–89	...	..	..	..	1	..	...	..	..	6	6	17
90–93	...	..	..	..	..	..	...	..	..	2	4	8
94–97	...	..	..	..	..	..	...	..	..	5	4	3
98–101	...	..	..	..	..	..	..	..	..	1	13	..
102–105	...	..	..	..	..	..	...	..	..	2	11	..
106–109	...	..	..	..	..	..	...	..	..	..	10	..
110–113	...	..	..	..	..	..	...	..	..	..	9	..
114–117	...	..	..	..	..	..	...	..	..	..	9	..
118–121	...	..	..	..	..	..	...	..	..	..	2	..
Total	206	83	183	206	83	183	408	135	56	249	84	183
Av.(M)	25.0	31.8	26.2	43.2	67.2	42.0	37.3	49.1	36.6	67.2	99.1	68.0
PE_M	.21	.25	.16	.41	.76	.56	.17	.38	.25	.46	.95	.70
No. males	89	67	92	89	67	92	24	102	32	89	67	92
Av.	25.0	31.9	26.5	45.6	68.2	44.7	40.5	48.9	36.6	70.7	100.5	71.5
PE_M	.36	.25	.22	.65	.87	.87	.63	.47	.34	.78	1.00	1.06
No. females	97	16	91	97	16	91	35	33	24	102	16	91
Av.	25.4	31.1	25.5	43.1	61.8	38.7	42.0	49.5	37.0	67.9	93.2	64.5
PE_M	.23	.54	.20	.56	2.12	.68	.50	.62	.30	.77	2.39	.85

* Age determined for all specimens by an examination of scales, except for some less than 40 mm. long, and except for 37 of the pumpkinseeds, all of which were near the modal size for the yearling group. The method of growth computation, by use of scales from yearlings, is explained in the text.

part of the observed difference in size of the yearling fish is evident from the fact that even the female hybrids average larger than the males of the parent species at this age. The data for these statements appear at the bottom of Table V.

The data for Crystal Lake, though very gratifying on account of the large numbers of specimens involved and the clear statistical significance of the observed differences, apply only to the first two growing seasons. It is important to determine whether this difference in growth rate is maintained through life in order to produce very large hybrids, or whether the growth curve of

TABLE VI

Excess in Growth of Hybrids over That of Parent Species, and Number of Times the Differences Exceed the Probable Error of the Differences (Data from Table V)

	Computed growth				Measured size			
	First year (1930)		Second year (1931)		Young of year		Yearlings	
	Hybrids and pumpkinseeds	Hybrids and bluegills	Hybrids and pumpkinseeds	Hybrids and bluegills	Hybrids and pumpkinseeds	Hybrids and bluegills	Hybrids and pumpkinseeds	Hybrids and bluegills
Difference (Δ)	6.8	5.6	24.0	25.2	11.8	12.5	31.9	31.1
$\frac{\Delta_M}{PE_{\Delta_M}}$	21	19	28	27	28	28	30	29

the hybrids breaks more abruptly. Unfortunately, the evidence available to us is meager. This is shown in Table VII.

Though decidedly insufficient, the available data do seem to show that the increased growth of the hybrids between *Eupomotis* and *Helioperca* is maintained. The large size of the three-year-old hybrids from Sunken Lake is much accentuated by their excessively heavy build, and especially by their very gibbous napes and throats, the exaggerated male characters to which we have already referred.

TABLE VII

SIZES OF HYBRID SUNFISH, *EUPOMOTIS GIBBOSUS* × *HELIOPERCA INCISOR*, AND OF PARENT SPECIES, FROM THIRD SISTER LAKE, MICHIGAN (COLLECTIONS OF JUNE, 1931) AND FROM SUNKEN LAKE, MICHIGAN (COLLECTIONS OF JULY 17 AND SEPTEMBER 17, 1925)

LENGTHS TO CAUDAL

Age III, Third Sister Lake	*Eupomotis:* — HYBRID: 60 mm. *Helioperca:* 51, 52 mm. (av., 51.5 mm.)
Age IV, Third Sister Lake	*Eupomotis:* 66, 71, 79 mm. (av., 72.0 mm.) HYBRIDS: 56, 63, 65, 102, 110, 111 mm. (av., 84.5 mm.) *Helioperca:* 60 to 100 mm. (57 specimens; av., 74.4 mm.)
Age I, Sunken Lake	*Eupomotis:* 27 to 62 mm. (42 specimens; av., 50.3 mm.) HYBRIDS: — *Helioperca:* 59 mm.
Age II, Sunken Lake	*Eupomotis:* 62, 73, 75, 76, 76, 78, 83, 84, 86, 87, 94 mm. (av., 79.5 mm.) HYBRIDS: — *Helioperca:* —
Age III, Sunken Lake	*Eupomotis:* — HYBRIDS: 120, 156, 158, 160 mm. (av., 148.5 mm.) *Helioperca:* —
Age IV, Sunken Lake	*Eupomotis:* 114 mm. HYBRIDS: — *Helioperca:* —

Eupomotis gibbosus × *Xenotis megalotis peltastes*

The growth of this hybrid combination is of especial interest in that one of the forms, *Xenotis*, is greatly dwarfed in Michigan. The hybrids do not appear to be half-dwarfed (in agreement with their otherwise intermediate characters). On the contrary, they appear to grow to as large a size as does the larger species. The data, admittedly meager, are shown in Table VIII. It seems certainly clear, however, that the hybrids grow to a vastly larger size than do the long-eared sunfishes (*Xenotis*) in the same localities. Nowhere in Michigan does this dwarfed subspecies of the long-eared sunfish grow as large as the hybrids.

TABLE VIII

COMPARISON BETWEEN SIZES OF HYBRIDS, *EUPOMOTIS GIBBOSUS* × *XENOTIS MEGALOTIS PELTASTES*, AND OF PARENT SPECIES OCCURRING AT SAME LOCALITIES (ALL IN MICHIGAN). LENGTHS TO CAUDAL

Most of the *Xenotis* specimens were breeding fish at each locality

Pine River, near Alma	*Eupomotis:* — HYBRID: 121 mm. (ripe female) *Xenotis:* 76 mm. (breeding male)
Ross Lake, Gladwin Co.	*Eupomotis:* 226 specimens; largest 154 * mm. HYBRIDS: 86, 113, 131 mm. *Xenotis:* 418 specimens; largest 105 † mm.
Grousehaven, Ogemaw Co.	*Eupomotis:* 90 specimens; largest 128 mm. HYBRIDS: 119, 130, 144, 147, 148, 160 mm. *Xenotis:* 71 specimens; largest 58 mm.
Beaver L., Montmorency Co.	*Eupomotis:* — HYBRID: 107 mm. *Xenotis:* 2 specimens; larger 57 mm.
Twin L., Montmorency Co.	*Eupomotis:* 20 specimens; largest 128 mm. HYBRID: 55 mm. *Xenotis:* —

* Only three more than 120 mm. long.
† Only one more than 82 mm. long.

Apomotis cyanellus × *Xenotis megalotis peltastes* [3]

The growth of these hybrids is of even greater interest, inasmuch as in Michigan both parent species are usually much dwarfed. We do not have enough material on these hybrids on which to base a reliable age study. Furthermore, age studies based on specimens, taken in summer, of miscellaneous species from different localities are always subject to some doubt. We are able to show, however, that these hybrids attain a decidedly

[3] In 1932 we have succeeded in obtaining eggs from three aquarium matings of these two species. From two sets of eggs (from identical parents) a few young escaped death from fungus epidemics, and five from one set of eggs have developed into fish intermediate between the parent species in structure, form and color, except that they are brighter, especially on the reddish fins. They are sufficiently like the natural hybrids to prove the hybrid origin of the latter.

larger size than either of the parent species ordinarily does, whether at the same locality or elsewhere in the state (Table IX).

TABLE IX

Comparison between Sizes of Hybrids, *Apomotis cyanellus* × *Xenotis megalotis peltastes*, and of Parent Species Occurring at the Same Localities, All in Michigan. Lengths to Caudal

Most of the *Xenotis* specimens were breeding adults

Ross Lake, Gladwin Co.	*Apomotis:* — Hybrids: 80, 80, 86, 102, 104, 105, 113, 113, 113, 118, 136, 147 mm. *Xenotis:* 418 specimens; largest 105 mm.*
Mill Lake, Newaygo Co.	*Apomotis:* 7 specimens, largest 103 mm. Hybrids: 64, 75, 75, 85, 88 mm. *Xenotis:* 6 specimens; largest 72 mm.
Blue Lake, Newaygo Co.	*Apomotis:* — Hybrids: 83, 89, 92 mm. *Xenotis:* —
Silver Lake, Washtenaw Co.	*Apomotis:* 6 specimens; largest 54 mm. Hybrid: 79 mm. *Xenotis:* 27 specimens; largest 66 mm.

* Only one longer than 82 mm.

To show to what degree *Apomotis* and *Xenotis* are dwarfed in Michigan, we give in Table X the size frequencies of the largest specimen in each collection from the state, in the University of Michigan Museum. Among the 1,245 specimens of *Xenotis megalotis peltastes* in this tabulation, largely mature fish, only three are longer than 93 mm. to the caudal: a female from Ross Lake, 105 mm. long, and two 108 and 109 mm. long, from the southern tier of counties, from which we have no hybrids. Out of 701 Michigan examples of *Apomotis cyanellus*, only four are longer than 140 mm. to caudal, and of these three came from one southern lake in a region of good fish growth, from which we have no hybrids.

II. Predominant Maleness of the Hybrids

A disturbed sex ratio is a frequent result of interspecific hybridization. Such hybrids in birds, for instance, have been

TABLE X

SIZE FREQUENCIES OF LARGEST SPECIMEN OF HYBRID SUNFISH, *APOMOTIS CYANELLUS* × *XENOTIS MEGALOTIS PELTASTES*, AND OF THE PARENT SPECIES, IN EACH MICHIGAN COLLECTION EXAMINED

Entries made irrespective of age or maturity

Length to caudal to nearest 5 mm.	Largest specimen in each collection		
	Apomotis	Hybrid	*Xenotis*
20	5	..	..
25	2	..	..
30	3	..	..
35	1	..	3
40	6	..	2
45	5	..	4
50	10	..	1
55	4	..	7
60	5	..	7
65	2	..	10
70	3	..	13
75	6	..	5
80	2	1	2
85	2	..	3
90	1	2	1
95	1	..	1
100	3	1	..
105	1	..	1
110	5	..	2
115	2	..	..
120	1	..	..
125	1	..	..
130	2	..	..
135	1	..	..
140	1	..	..
145	..	1	..
150	..	..	..
155	1	..	..
160	..	..	..
165	..	..	..
170	..	..	..
175	..	..	..
180	..	..	..
185	..	..	..
190	2	..	..

shown to be predominantly of the male sex (Guyer, 1909). Haldane (1922) has explained the unbalanced sex ratio as related to the sex-determining mechanism, on the basis of the greater viability of the homozygous sex. Thomas and Huxley (1927) favor a sex-reversal explanation. Whatever the explanation or generalities may be, it seems clear that hybrid sunfish of at least most combinations are predominantly males.[4]

The high male ratio holds for both the aquarium-reared and nature-reared hybrids, as shown in Table XI. The similarity in the observed sex ratios of the two series is a further demonstration of their identity and, as a corollary, of the true hybrid character of the specimens caught in nature.

TABLE XI

Sex Ratio of Aquarium-reared and Nature-reared Hybrid Sunfish

	Males	Females	Percentage of males
Apomotis cyanellus × *Eupomotis gibbosus*			
Aquarium-reared	38	2	95
Nature-reared	295	17	95
Apomotis cyanellus × *Helioperca incisor*			
Aquarium-reared	35	8	81
Nature-reared	47	11	81
Apomotis cyanellus × *Xenotis megalotis peltastes*			
Aquarium-reared	5*	1	83
Nature-reared	20	2	91

* In one of these males the testis contained what appeared to be a few ova.

The predominant maleness of hybrids presumably characterizes both reciprocal crosses of any combination. For the *Apomotis* ♂ × *Eupomotis* ♀ cross all three offspring sexed were males. Of the *Eupomotis* ♂ × *Apomotis* ♀ progeny 35 were males and 2 were females.

[4] The sex was determined by an examination of the gonads. When any doubt existed, a bit of the gland was teased out and examined under a compound microscope. Furthermore, a considerable number of gonads were sectioned and stained. Most of this work was done for us by Chester A. Lawson.

General experience and a considerable number of counts (Table XII) have shown that the sexes in Centrarchidae normally exist in about equal numbers.

TABLE XII

Sex Ratio of Two Species of Sunfish from Michigan

	Males	Females	Percentage of males
Eupomotis gibbosus			
Willow Run, near Ypsilanti	102	102	50
Crystal Lake, Oceana Co.			
Young	24	35	41
Yearlings	92	104	47
Total for species	218	241	47
Helioperca incisor			
Crystal Lake, Oceana Co.			
Young	32	24	57
Yearlings	93	92	50
Total for species	125	116	52

As shown in Table XIII and in Figure 71, predominant maleness characterizes most if not all of the presumed hybrid combinations of sunfishes found in nature. This is indicated for all combinations for which a reliable number of counts have been obtained, and for some combinations represented by only a few individuals. For a few of the rare combinations the females in our counts outnumber the males, and it is quite possible that in these, especially in the cross *Xenotis* × *Eupomotis*, the sex ratio may not be overbalanced toward the male side. It will be interesting to obtain further evidence on the sex ratio of this hybrid, from nature-taken specimens, or, better, from aquarium-reared ones.

The predominant maleness shown by the supposed hybrid combinations, which we have not as yet been able to duplicate by experimental breeding, we take as very strong evidence for the correctness of the view that they are true hybrids.

III. Apparent Sterility of the Hybrids

As our work has progressed, the evidence has become stronger and stronger that most if not all of the sunfish hybrids are infertile. This evidence will now be considered.

TABLE XIII

SEX RATIO OF SUPPOSED HYBRID SUNFISHES CAUGHT IN NATURE*

Hybrid combination and locality	Males	Females	Percentage of males
Chaenobryttus gulosus × *Apomotis cyanellus*			
Big Swamp Creek, Alabama	...	2	0 (?)
Chaenobryttus gulosus × *Helioperca incisor*			
Georgia and Alabama	4	...	100 (?)
Chaenobryttus gulosus × *Eupomotis gibbosus*			
Newaygo Co., Michigan	...	1	0 (?)
Apomotis cyanellus × *Xenotis megalotis breviceps*			
Comanche Co., Oklahoma	1	...	100 (?)
Apomotis cyanellus × *Xenotis megalotis megalotis*			
Quincy, Illinois	1	...	100 (?)
Apomotis cyanellus × *Xenotis megalotis peltastes*			
Ross Lake, Gladwin Co., Michigan	11	1	92
Newaygo Co., Michigan	8	...	100
Miscellaneous, Michigan	1	1	50 (?)
TOTAL	20	2	91
Apomotis cyanellus × *Xenotis megalotis* (all subspecies):	22	2	92
Apomotis cyanellus × *Helioperca incisor*			
Miscellaneous, Michigan	7	1	87
Wisconsin, Ohio, Nebraska, Missouri	3	2	60
"Osage River, Arkansas"[= Missouri?]	18	4	82
Arkansas	13	3	81
Texas	6	1	84
TOTAL	47	11	81
Apomotis cyanellus × *Allotis humilis*			
Little River, Oklahoma	1	1	50 (?)
Apomotis cyanellus × *Eupomotis gibbosus*			
Wiard's Pond, Michigan	20	...	100
Willow Run, Michigan	46	6	88
Middle River Rouge, Michigan	196	8	96
Phoenix Pond, Michigan	6	1	86
Newaygo Co., Michigan	17	2	89
Miscellaneous, Michigan	8	...	100
Wisconsin	2	...	100 (?)
TOTAL	295	17	95
Lepomis auritus × *Eupomotis gibbosus*			
New York (state)	3	1	75 (?)
Xenotis megalotis haplognathus × *Helioperca incisor*			
Rio San Juan, Tamaulipas	...	1	0 (?)

Hybrid combination and locality	Males	Females	Percentage of males
Xenotis megalotis breviceps × *Helioperca incisor*			
West Cache Creek, Oklahoma	2	...	100 (?)
Xenotis megalotis peltastes × *Helioperca incisor*			
Pettibone Creek, Michigan	1	...	100 (?)
Xenotis megalotis (all subspecies) × *Helioperca incisor*	3	1	75 (?)
Xenotis megalotis peltastes × *Eupomotis gibbosus*			
Ross Lake, Gladwin Co., Michigan	2	1	67
Pine River, near Alma, Michigan	...	1	0 (?)
Ogemaw Co., Michigan	1	5	17
Montmorency Co., Michigan	2	...	100 (?)
TOTAL	5	7	42
Helioperca incisor × *Eupomotis gibbosus*			
Crystal Lake, Oceana Co., Michigan			
Young	103	33	76
Yearlings	72	17	81
Newaygo Co., Michigan	12	1	92
Ogemaw Co., Michigan	7	1	87.5
Carp Lake, Emmet Co., Michigan	6	2	75
Miscellaneous, Michigan	35	5	87.5
Wisconsin	2	...	100 (?)
TOTAL	237	59	80
GRAND TOTAL, ALL HYBRIDS (including those aquarium-reared)	695	113	86

* Some additional specimens have been sexed since Figure 71 was prepared. Consequently the figures given there and in this table are not in full agreement.

The remarkable uniformity of the natural hybrids, not duly appreciated in the early stages of our work, suggests that they are consistently F_1 hybrids. The characters of the hybrids do not grade into those of either parent species. The examination of hundreds of specimens of each of three combinations has so familiarized us with the hybrid characters that we recognize new specimens with the same facility and certainty with which a trained systematist identifies well-known species. In a later contribution we expect to analyze the hybrid characters statistically; for the present we shall have to ask that these statements be accepted.

The failure of certain sunfish hybrids of the *Apomotis* × *Eupo-*

motis combination to reproduce was first forcibly brought to our attention on hearing an experience of fish culturists. For two years several hundred sunfish, shown later by us to be nearly all hybrids of this combination, had been kept in one of the

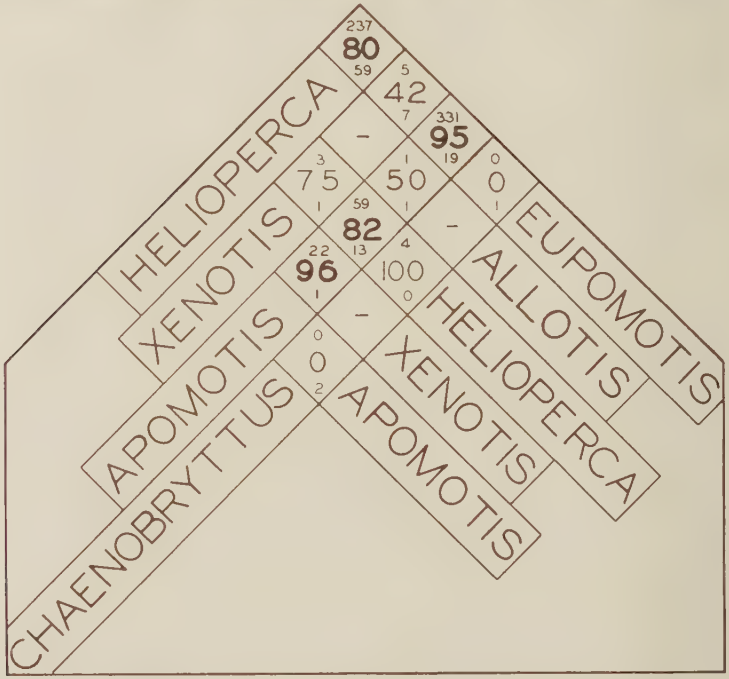

Fig. 71. Sex ratios for hybrid sunfish of ten intergeneric combinations. Data from aquarium-reared sunfish as well as from those taken in nature. The middle figure in each diamond indicates the percentage of males of the given combinations; the upper and lower figures indicate the number of males and females sexed. The data have been somewhat expanded since the figure was drawn (see Table XIII)

ponds of the Northville Fish Hatchery of the Bureau of Fisheries. Although these sunfish were reported to have been very active in their nest building all through the warm season, no progeny were obtained either year. This failure was not due wholly to the predominant maleness of the hybrids, for we found some

females among them, and there were some individuals of the parent species in the same pond.

The very fact that the *Apomotis* × *Eupomotis* hybrids engaged in their nesting performances all summer long was in itself evidence of something wrong in their sexual make-up. We have since verified this prolonged nesting behavior, in aquaria, in our wire pens (4 × 8 feet) in Third Sister Lake and in a garden fish pond. Under outdoor conditions some of the hybrids of this combination were observed to remain on their cleared redds and to guard them from early in the season until well into October, not deserting their work and vigil until the water had been chilled to below 50° F.

Another indication of unnatural sexual behavior among the *Apomotis* × *Eupomotis* hybrids was exhibited by an aquarium-bred individual which played the part of a female in an attempted mating, vigorously taking the initiative in the female nuptial behavior. Yet a superficial and histological examination of the gonads of this fish showed it to be a male. One of the few females of this same combination which we have been able to keep under observation repeatedly dug nests and otherwise played the part of the male in nesting and mating behavior. A male *Apomotis* × *Helioperca* behaved as a female.

Although the *Apomotis* × *Eupomotis* hybrids go through all the ordinary preliminaries of the breeding behavior, in fact show an apparent excess in nuptial vigor, it is very seldom indeed that milt can be stripped even from a nest-building male. This is most unusual, for ordinarily milt can be made to flow freely from any nest-building sunfish. About two hundred nest-building males of this hybrid combination have been tried, some of the individuals several times, yet only two have yielded milt. One of these was an aquarium-raised fish, from which a very small amount of milt was stripped, on two occasions only, when it was between sixteen and seventeen months old, and again when it was twenty-eight months old.

We have not yet succeeded in stripping milt from any *Apomotis* × *Helioperca* hybrids, either the natural or the aquarium specimens, although a number have made nests.

On several occasions a male hybrid in nuptial inactivity was given an injection of the pituitary gland of either another hybrid individual or of one of the parent species. Nuptial behavior, marked especially by vigorous nest building, was thus initiated within one or a few days. But these individuals showed no milt on attempted stripping.

The few adult female hybrids used in our experiments could be stripped with ease. In fact, the ova appeared to run more freely on abdominal stroking than those of the pure species. But these ova appeared distinctly abnormal, showing very little structure, appearing like transparent bladders blown tightly full with water. These ripe female hybrids were a few specimens of *Apomotis* × *Eupomotis* and of *Eupomotis* × *Helioperca*. An aquarium-bred female *Apomotis* × *Helioperca* naturally spawned similar ova.

The milt from the one aquarium-reared *Apomotis* × *Eupomotis* which could be stripped presented some clear indications of abnormality. Although a few of the spermatozoa seemed to be of normal size and motility, most of them were variously larger and more sluggish. Extreme ones, with an almost spherical sperm head several times as large as the normal, were barely rolled along by the lashing of the sperm tail. These were apparently giant sperm, such as described by Meves (1903) for *Paludina* and *Pygaera* and by Geoffrey Smith (1912) for hybrid pigeons. We have never pressed such structures from a pure species of sunfish, or from any other fish. Normally, the sperm heads of sunfish are very minute, somewhat oval, and, so nearly as can be judged, uniform in size.

In a stained section of the testis of a hybrid *Helioperca incisor* × *Xenotis megalotis peltastes* we find sperm ducts filled with similar spermatozoa (Pl. LXV, Fig. 3). The extreme variability in size of these spermatozoa and the relatively gigantic size of some are appreciated on comparing the figures of these spermatozoa with those of one of the parent forms (*Helioperca*), as shown in Figure 4.

In other slides of testes of hybrid sunfishes showing spermatogenesis we find a similar variation in size of nuclei in the later

stages of spermatogenesis. Within single tubules the nuclei may vary greatly not only in size (up to 300 per cent), but also in shape, structure, and degree of compactness or fragmentation. We have found this variation in several of the intergeneric combinations, as *Allotis* × *Apomotis*, *Apomotis* × *Eupomotis*, *Apomotis* × *Helioperca*, *Eupomotis* × *Xenotis*.

In the combination *Eupomotis* × *Helioperca* we noted (Hubbs, 1920) that in specimens of adult size the testis may be represented by a mere strand of tissue, or may be well developed. On making slides of other specimens we find evidence of further testis variation in this hybrid combination. In some individuals we find spermatogenesis proceeding through the testis (probably leading to variable sperm). In one example, however, there is an entirely different picture (Pl. LXV, Figs. 1–2), quite unlike normal sunfish spermatogenesis (Fig. 4). Very few normal primordial germ cells are apparent, and no clear stages in spermatogenesis are obvious. This circumstance cannot be due to poor fixation, because the testis, first removed from a live fish, was divided and then carried through several standard fixing and staining techniques (by Mr. Chester A. Lawson). The tubules were lined by a more or less regular epithelium instead of by normal germ-cell structure. The epithelial cells perhaps represent modified germ cells, since transitional stages appear to be presented by other individuals. Or they may represent modified interstitial cells. In either event the cell structure is obviously abnormal, and the fish is infertile. These epithelial cells show various stages of enlargement and degeneration. Many nuclei may be observed in apparent stages of disintegration. The cytoplasm in many cells forms a loose reticulum, which is often difficult to observe. Elsewhere may be seen hollow alveoli, in which the process of protoplasmic degeneration appears to have been completed.

In several of the aquarium-reared specimens of *Apomotis* × *Helioperca* of adult size the testis was a mere strand of tissue. In a half-grown hybrid resulting from the crossing of a male *Apomotis* with a female *Eupomotis* no gonad whatever could be located.

The only evidence for sex intergrades obtained was the doubt-

ful case of one of the aquarium-reared *Apomotis* × *Xenotis*, which had what appeared to be a testis containing a few ova. The specimen, however, was small and poorly preserved.

No evidence for sex reversal was obtained.

The abnormality and variability in the histology and the cytology of the sperm of sunfishes not only is related to their infertility, but also serves as a clear verification of our interpretation of their hybrid nature. It will be noted that the abnormalities were observed (and are figured) for hybrid combinations, which we have not verified experimentally. No such abnormalities were observed in sections of testes of species of *Apomotis*, *Eupomotis*, *Helioperca*, and *Micropterus*.

A. ATTEMPTED HYBRID MATINGS

Furthermore, all efforts to mate the hybrids with one another, with one of the parent species, or with still another species have yielded negative results, although full advantage was taken of the occasional maturing of hybrids, both males and females. These experiments are now briefly recounted.

1. (*Apomotis* × *Eupomotis*) ♂ × (*Apomotis* × *Eupomotis*) ♀

Experiment 18a. — The one aquarium hybrid male which had yielded milt and which had spawned previously with an *Apomotis* female (Experiment 11) was mated on June 13, 1931, with a large hybrid female recently taken in Third Sister Lake. The male was again yielding milt and proceeded at once to the construction of his redd. The female, though not distended, yielded eggs on pressure. The larger female was very rough on the male, so that we separated them two days later for fear he might be killed. Five and seven days later this hybrid male spawned with two females of *Apomotis* (Experiments 18*b* and 18*c*).

Experiment 33. — On June 23, 1931, the same male was placed with a mature female hybrid of the same combination, which had been taken the day previous in Middle River Rouge. Although the male proceeded almost immediately to nest-building, no eggs were laid.

2. (*Apomotis* × *Helioperca*) ♂ × (*Apomotis* × *Helioperca*) ♀

Experiment 30. — On the morning of June 22, 1931, after several of the green sunfish by bluegill hybrids of the second aquarium brood (Hubbs and Hubbs, 1932) had been redd-building for a week, one nest was found sprinkled with a few eggs, guarded by a medium-sized male. These eggs must have been laid by one of the brood. When examined later the same day, they were found to be infertile and of the appearance already described.

B. ATTEMPTED BACKCROSSES

3. (*Apomotis* × *Eupomotis*) ♂ × *Apomotis* ♀

Experiment 11. — The male hybrid used later in Experiments 18*a* and 33 discussed above, when ripe on July 3, 1930, was placed with a small, ripe green sunfish taken near Ann Arbor. Two days later he cleared a small nest, but was languid in his interest; in two more days he had cleaned out a larger nest which was found in the morning liberally sprinkled with eggs. The eggs, showing no segmentation, became fungused the next day.

Experiment 14. — A male hybrid from Middle River Rouge, induced into nest-building activity by pituitary injection but not yielding milt on pressure, was placed with a nearly mature green sunfish female from Illinois, on March 20, 1931. So vigorous were his efforts to force the female to spawn that he promptly murdered her.

Experiment 15. — One of the aquarium-bred *Apomotis* × *Eupomotis* males, brought up to nuptial activity by pituitary injection, similarly disposed of his green sunfish mate.

Experiments 18b and c. — Immediately after Experiment 18*a* recounted above, the ripe male hybrid spawned under our observation with a small green sunfish female on June 20, and two days later spawned with another small green sunfish mate, like the other from near Ann Arbor. The eggs gave clear indications under the microscope of being infertile, since they were of abnormal appearance and failed to show any indication of development.

4. *Apomotis* ♂ × (*Apomotis* × *Eupomotis*) ♀

Experiment 37. — The reciprocal backcross was attempted July 31, 1931, with the male green sunfish which had spawned successfully with a pumpkinseed sunfish on June 13, but which was now fully ripe again. The mate was a fully ripe female hybrid, originally from Middle River Rouge. No egg-laying resulted.

5. (*Apomotis* × *Eupomotis*) ♂ × *Eupomotis* ♀

Experiment 23a. — The hybrid male used in Experiment 15 was mated with a ripe pumpkinseed female from Frain's Lake, near Ann Arbor, on June 17, 1931. Although the mate was larger, he abused her so violently that she died within a few days, still full of eggs.

6. (*Apomotis* × *Helioperca*) ♂ × *Apomotis* ♀

Experiment 17. — On June 13, 1931, a nest-building male hybrid, green sunfish by bluegill, from Middle River Rouge, was mated with a mature green sunfish from Third Sister Lake. Although no milt could be extruded from the male, he cleared a fine redd within an hour. The nest was found covered with eggs six days later, in the morning, and more were deposited the next day. None, however, showed any signs of development, and all soon died.

7. (*Apomotis* × *Helioperca*) ♂ × *Helioperca* ♀

Experiment 27. — The other backcross was attempted in June, 1931, with a male from Middle River Rouge and two females from Frain's Lake, all mature. No results, except for the killing of both females.

C. ATTEMPTED OUTCROSS

8. (*Apomotis* × *Eupomotis*) ♂ × *Helioperca* ♀

Experiment 23b. — After Experiment 23, as described above, a bluegill mate was offered to the hybrid male, but she, too, was promptly killed.

Summary

INCREASED GROWTH OF THE HYBRIDS

1. The aquarium-produced hybrid sunfish, *Apomotis* × *Helioperca*, grew to an average standard length of 96.5 mm. in twenty-two months, when the largest were more than 8 inches long.

2. An aquarium-produced *Apomotis* × *Eupomotis* hybrid reached 99 mm. in nine months, when it was found building a nest.

3. Natural hybrids of this combination in two additional collections averaged slightly larger than the parent species taken with them.

4. Decisive evidence that the natural hybrids *Eupomotis* × *Helioperca* grow faster than their parent species is presented.

5. This greater growth occurred during a year of poor growth and in a year of good growth.

6. Scattering evidence indicates that the increased growth of hybrid sunfish is continued through life to produce very large adults.

7. Crosses with or between dwarfed sunfish forms produce hybrids which are not notably dwarfed.

PREDOMINANT MALENESS OF THE HYBRIDS

8. Both aquarium-reared and natural hybrids, *Apomotis* × *Eupomotis*, *Apomotis* × *Helioperca*, and *Apomotis* × *Xenotis*, are predominantly males (81 to 95 per cent).

9. The pure species have no such disturbed sex ratio.

10. Similar high male ratios were obtained for other (presumed) hybrid combinations, of which a sufficient number of specimens are available.

11. In a few of the rarer combinations the males may not predominate.

APPARENT STERILITY OF THE HYBRIDS

12. The hybrids are indicated as sterile by: (*a*) their remarkable uniformity; (*b*) their failure to reproduce in ponds; (*c*) their unnatural spawning behavior; (*d*) the rareness of males

from which milt can be stripped; (*e*) the failure of pituitary injection to produce more than secondary nuptial behavior; (*f*) the bladder-like ova of ripe females; (*g*) the strandlike testis of some hybrids (gonad apparently absent in rare instances); (*h*) the abnormal (huge) sperm of the one ripe male studied; (*i*) abnormal variation in size, shape, and structure of nuclei in late stages of spermatogenesis; (*j*) degenerative germ-cell structure in at least some males; (*k*) the failure of attempted hybrid matings, backcrosses, and one outcross to produce any results, even though eggs were deposited several times.

ADDITIONAL CONCLUSIONS

13. In computing past growth of sunfish from scale measurements a correction needs to be added to the growth-computation formula.

14. The intergeneric hybrid *Apomotis* × *Xenotis*, in addition to two other combinations previously reported, has now been confirmed by an aquarium mating.

University of Michigan

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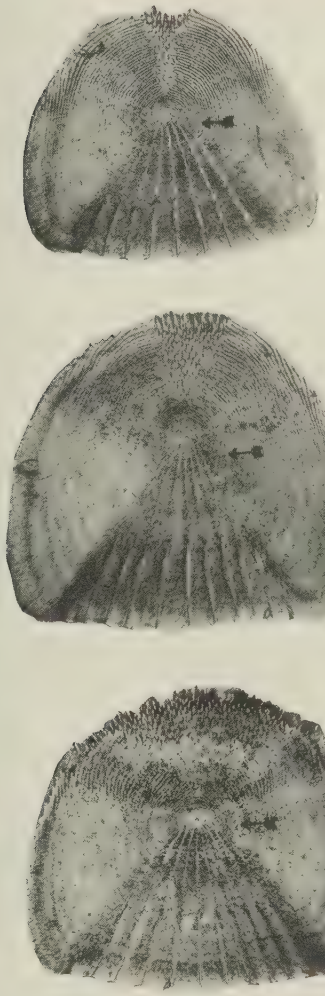
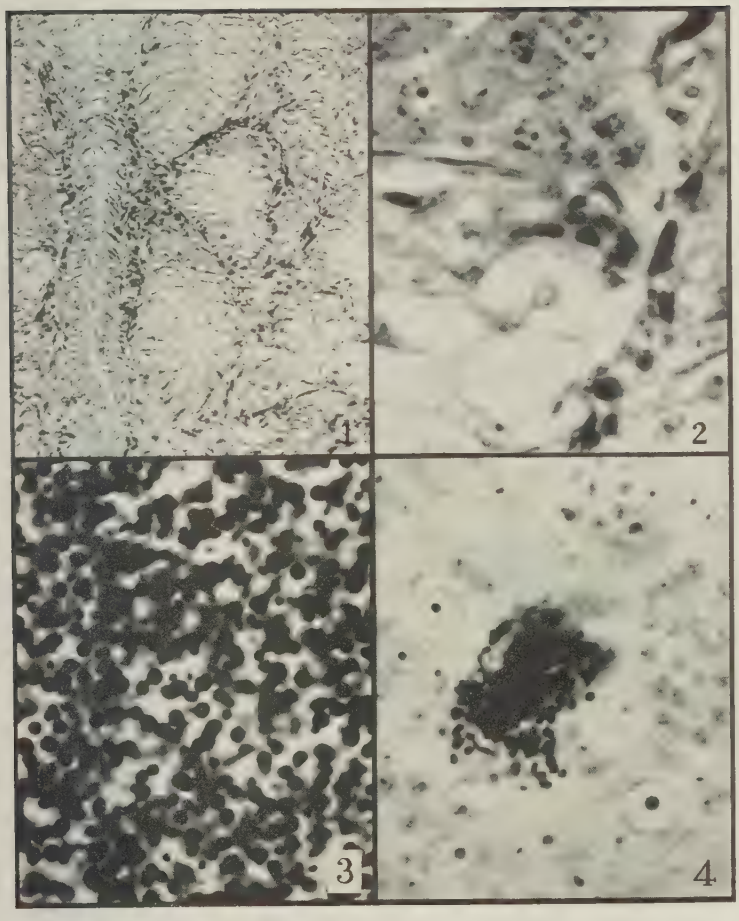
PLATE LXIV



Scales of fish from Crystal Lake collection of October 25, 1931: *A*, hybrid sunfish (*Eupomotis* × *Helioperca*); *B*, pumpkinseed (*Eupomotis*); *C*, bluegill (*Helioperca*). All scales from yearlings. The arrows point to the first winter marks, the positions of which indicate the poor growth of 1930 and the good growth of 1931

PLATE LXV



SECTIONS OF TESTES OF ADULT HYBRID SUNFISHES AND OF A PARENT SPECIES

FIG. 1. *Eupomotis gibbosus* × *Helioperca incisor*. Section of testis showing degeneration of cells forming an epithelium in the tubules. × 200

FIG. 2. *Eupomotis gibbosus* × *Helioperca incisor*. Portion of same section. × 1230

FIG. 3. *Helioperca incisor* × *Xenotis megalotis peltastes*. Spermatozoa of varying sizes loose in the testis duct. × 1230

FIG. 4. *Helioperca incisor*. Spermatozoa of uniform and small size in the testis duct. × 1230

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PRELIMINARY REPORT ON THE AGE AND GROWTH OF THE YELLOW PERCH (*PERCA FLAVESCENS* MITCHILL) FROM LAKE ERIE, AS DETERMINED FROM A STUDY OF ITS SCALES *

FRANK W. JOBES

THE yellow perch (*Perca flavescens* Mitchill) is one of the abundant commercial fishes of Lake Erie, and is of some commercial importance in certain sections of Lakes Huron and Michigan. It is also common in most of the inland lakes of the Great Lakes basin.

Studies have been made on the life-history and growth of the yellow perch from some of these lakes, but up to the present time only one paper has been published on their growth in the Great Lakes.[1] A review of the literature and of the methods of age determination from scales will be deferred to a later paper. This report assumes the validity of the scale method and theory.

MATERIALS

Age determinations and growth computations have been made from the scales of 1,170 yellow perch collected during the seasons of 1927 and 1928 from the commercial trap nets fished out of Sandusky, Lorain, and Ashtabula. All these ports are located on Lake Erie in the State of Ohio. The 1927 data are based on 481 perch taken in six collections from October 24 to November 21; the 1928 data, on 689 perch taken in six collections from July 17 to November 20.

* Published with the permission of the United States Commissioner of Fisheries.

[1] Harkness, W. J. K., "The Rate of Growth of the Yellow Perch (*Perca flavescens*) in Lake Erie," *Univ. of Toronto Studies, Biol. Series* No. 20 : 89–95. Publications of the Ontario Fisheries Research Laboratory, No. 6. 1922.

METHODS

Scales were removed from the left side of the fish, below the lateral line and about midway between the tip of the snout and the base of the caudal fin. The scales from each fish were placed in a small envelope on which data on the following items were recorded: locality, date, standard and total lengths, weight, sex, stage of maturity, type of gear used to catch the fish, collector, and a field number.

In the laboratory the scales were cleaned, and three from each fish were mounted on an ordinary glass microscopic slide in the gelatine-glycerine medium described by Van Oosten (1929, p. 275).[2] Data on the following items were written on the label of each slide: locality where collected, date of collection, standard length, weight, sex, stage of maturity, field number, and slide number. Most of the scales were studied by using a front-surfaced mirror-projection apparatus that gave a magnification of 42.75 diameters. Each scale was measured from the focus outward along the most anterior inter-radial space to each annulus and to the outside circulus. The growth of each year of life was computed by using the measurements in the following formula:

$$\frac{\text{Length of scale included in annulus } X}{\text{Total length of scale}} = \frac{\text{Length of fish at end of year } X}{\text{Length of fish at time of capture}}.$$

The ages were recorded by using numerals corresponding to the number of years that the individual fish had lived. Thus age-group 0 are those fish that were hatched the previous spring and show no completed annulus on their scales, and are, therefore, in their first year of life. Similarly, age-group II are those fish that are in their third year of life and show two completed annuli on their scales.

DISCUSSION

The age determinations suggest the presence of a dominant year-class in the Lake Erie perch in 1927 and 1928. The number

[2] Van Oosten, John, "Life History of the Lake Herring (*Leucichthys artedi* Le Sueur) of Lake Huron as Revealed by Its Scales, with a Critique of the Scale Method," *Bull. U. S. Bur. Fisheries*, 44 (1928) : 265–428. Document 1053, Washington. 1929.

of years during which this year-class predominates cannot be definitely stated until further studies have been completed.

TABLE I

PERCENTAGE OF THE TOTAL NUMBER OF YELLOW PERCH OCCURRING IN EACH AGE-GROUP FOR THE YEARS 1927 AND 1928

Year	Number of fish	Age-group				
		I	II	III	IV	V
1927	481	48.9	39.9	9.8	1.0	0.4
1928	689	1.6	90.4	7.4	0.6	...

The perch hatched in the spring of 1926 would be in age-group I in 1927 and in age-group II in 1928. From Table I it is seen that this 1926 year-class was the predominating group in both 1927 and 1928. The sharp increase in the percentage of abundance of age-group II in 1928 and the corresponding decrease in this percentage for age-group I is, no doubt, explained as being due to a very small year-class in 1927, so that relatively few fish in age-group I could be taken in 1928. (For the actual number of fish taken in each age-group see Table III.) It will be interesting to know whether the year-class of 1926 was also the predominating group in 1929 or whether the hatch in the spring of 1928 was sufficient to produce a one-year group in 1929 that outnumbered the three-year fish of the 1926 year-class.

Table II compares the growth-rates of the males and females for the second and third age-groups; Figure 72 shows graphically these growth-rates for the 1928 collection. A similar curve for the 1927 collections would show even less divergence than does Figure 72 in the growth-rates of the males and females taken during the season of 1927. From these data it appears that no consistent differences exist in the growth-rates of the two sexes. The calculated and actual standard lengths, as well as the increments of length of the two sexes of the two-year fish taken in 1928, are almost identical, although apparently insignificant differences exist in the growth values of the two sexes in the three-year fish taken

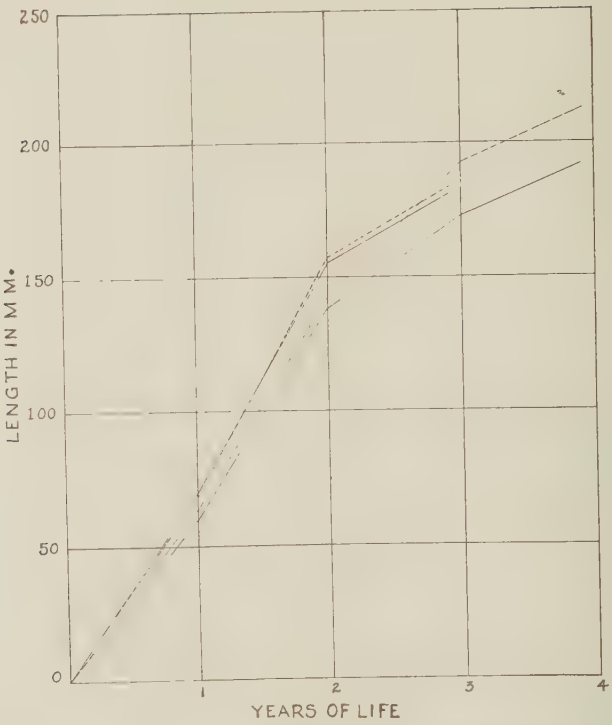

FIG. 72. Average standard length attained by the males and females of age-groups III and IV of the Lake Erie perch taken in 1928. The data are shown in Table II. —— males; ---- females

in 1927. The two-year perch taken in 1927 show a significant difference between the two sexes in the third year of life only, whereas the females of the three-year group of 1928 are consistently larger in each year of life than are the males of this group, but significantly so in the third and fourth years only. The consistent difference in the growth-rates of the two sexes found in the three-year group in 1928 may be explained in part as due to the small number of perch in this group, but this explanation cannot account for the great difference in the third year of life,

since a similar significant difference was found between the two sexes of this year-class collected as two-year fish in 1927.

A study of the increments of these age-groups in Table II reveals that the females in age-group II of 1927 grew 9 mm. more than did the males during their third summer in 1927, and that

TABLE II

CALCULATED STANDARD LENGTHS AND YEARLY INCREMENTS IN LENGTH OF THE YELLOW PERCH OF LAKE ERIE

Grouping is by sexes for the different age-groups and by the different years.

Year of capture	Age-group	Sex	Number of fish	Calculated length in mm. for age-groups				Increments in mm. for age-groups			
				0	I	II	III	0	I	II	III
1927	II	males	110	62	137	177*	...	62	75	40	..
1927	II	females	57	61	139	188*	...	61	78	49	..
1927	III	males	23	63	126	168	196*	63	63	42	28
1927	III	females	17	64	130	173	200*	64	66	43	27
1928	II	males	97	70	155	183*	...	70	85	28	..
1928	II	females	151	69	156	185*	...	69	87	29	..
1928	III	males	6	60	138	172	194*	60	78	34	22
1928	III	females	15	64	143	192	214*	64	79	49	22

* These lengths are actual; all others are calculated.

the females of age-group III of 1928 grew 15 mm. more than did the males in their third summer in 1927. Age-group II of the 1927 collection and age-group III of the 1928 collection are made up of fish of the same year-class (both belong to year-class 1925), and since the greatest difference in the growth-rates of the two sexes occurred in the third summer of life in these age-groups, the summer of 1927 is the only time during which the females grew at a rate that seems to be significantly greater than the rate of the males. The fish of the year-classes 1924 (the 1927 age-group III) and 1926 (the 1928 age-group II) do not show any apparently significant differences in the growth-rates of the sexes in 1927 or in any other calendar year. From this

it appears that the usual type of growth during the first four years of life is that in which the two sexes grow at approximately the same rates. No satisfactory reason can be assigned to explain just why the females of the 1925 year-class alone grew significantly faster than the males during 1927 only.

The curves of general growth of the Lake Erie yellow perch (Fig. 73) were made up from the combined collections of the

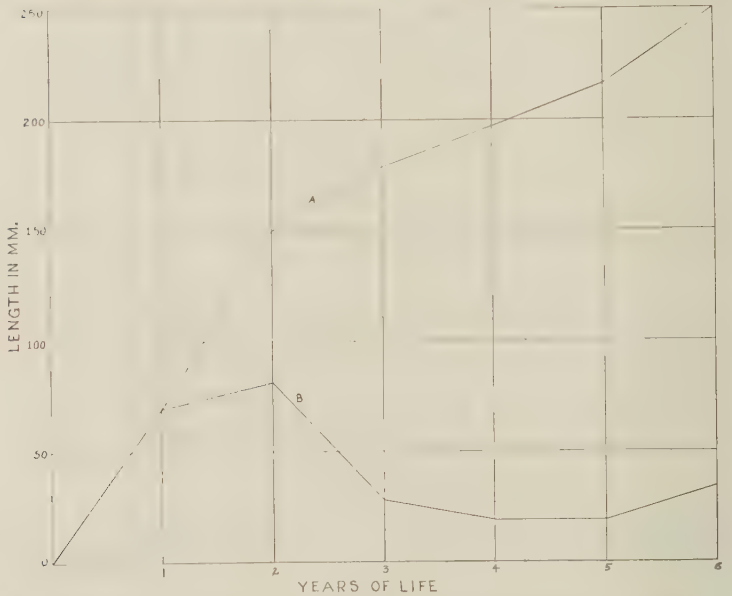

FIG. 73. Standard length (*A*) and increment in standard length (*B*) attained by Lake Erie perch at the end of each year of life. The curves are plotted from the grand averages of Table III

years 1927 and 1928 (see grand averages, Table III), and are based on the actual average standard-length measurements for the age-groups plus the average calculated growths for each year of life. The length values for each year's growth, except for age-group V, where only actual measurements are used, are in all probability too low because of the presence of "Lee's phe-

nomenon of apparent change in growth rate" in the calculated values of the 1927 collection.

TABLE III

THE ACTUAL AND CALCULATED AVERAGE STANDARD LENGTHS ATTAINED BY THE YELLOW PERCH IN LAKE ERIE IN EACH AGE-GROUP, ALSO THE AVERAGE ANNUAL INCREMENTS

Year of capture	Age-group	Number of fish in group	Length in mm. for age-groups					
			0	I	II	III	IV	V
1927	I	235	75	162*	...	...	...	...
1927	II	192	62	135	176*	...	...	...
1927	III	47	62	127	168	195*	...	...
1927	IV	5	65	122	165	189	214*	...
1927	V	2	66	127	177	209	231	250*
1928	I	11	69	140*	...	...	...	...
1928	II	623	70	154	178*	...	...	...
1928	III	51	69	139	178	198*	...	...
1928	IV	4	70	124	172	199	212*	...
GRAND AVERAGE			69	150	178	197	216	250
AVERAGE INCREMENT			69	81	28	19	19	34

* These lengths are actual: all others in the individual age-groups are calculated.

In the first two years of life the yellow perch has a standard-length growth curve with a slight upward trend from a straight line. In the first year the perch grows 69 mm. and in the second year 81 mm., attaining a standard length of 150 mm. at the end of the second year. There is a sharp break in the growth curve when the increment drops from 81 mm. in the second year to 28 mm. in the third year, and a much less decided break in the fourth year, when the increment is 19 mm. The annual increment remains at 19 mm. during the fifth year, but rises to 34 mm. during

the sixth year. The increase in growth-rate in the sixth year is no doubt due to the small number of fish employed. The standard length of 197 mm. reached by the perch in the fourth year of life is equivalent to a total length of nine inches, the legal size limit for perch in several of the Great Lakes states. The decided de-

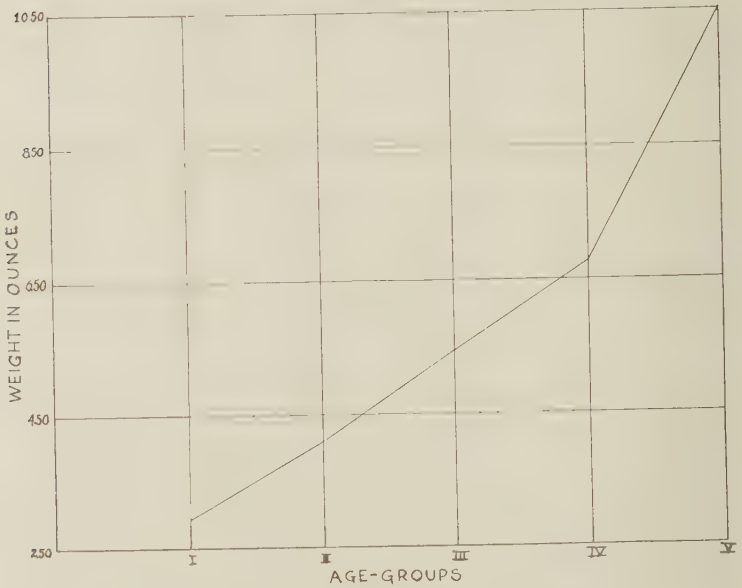

FIG. 74. Average weight, in ounces, attained by Lake Erie perch in the different years of life. The curve is plotted from the grand averages of Table IV, based on the collections of 1927 and 1928

crease in the growth-rate during the third summer may possibly be correlated with the attainment of sexual maturity.

The curve of the average weights of the age-groups shown in Figure 74 is based on the data of Table IV. Calculated weights have not been employed in this table. It is unknown, therefore, in what proportions the 2.92 ounces reached at the end of the second summer should be divided over the first two years. The weight of 4.11 ounces reached by age-group II represents a growth

increment of 1.19 ounces in the third year, whereas the average weight of age-group III of 5.42 ounces represents an increase of 1.31 ounces. The curve of growth based on the average weights has, therefore, a slight upward trend with a sharp rise from age-group IV to age-group V. This sharp rise may be due in part to the small number of fish used in obtaining the average weight in age-group V.

TABLE IV

AVERAGE ACTUAL WEIGHT IN OUNCES ATTAINED BY THE YELLOW PERCH IN LAKE ERIE

Year of collection	Age-group				
	I	II	III	IV	V
1927	2.96 (165)*	4.07 (192)	5.22 (47)	6.95 (5)	10.50 (2)
1928	2.32 (11)	4.12 (623)	5.60 (51)	6.48 (4)	.....
GRAND AVERAGE	2.92 (176)	4.11 (815)	5.42 (98)	6.74 (9)	10.50 (2)
AVERAGE INCREMENT	2.92	1.19	1.31	1.32	3.76

* Numbers of individuals employed are shown in parenthesis.

SUMMARY

Age and growth-rates have been determined for 1,170 yellow perch (*Perca flavescens* Mitchill) caught in the commercial trap nets of Lake Erie during the years 1927 and 1928. Of this total, 481 were taken in 1927, 689 in 1928. The youngest fish captured were in age-group I and the oldest in age-group V. The percentage of distribution of the groups is shown in Table I.

The year-class of 1926 formed the predominating group in the collections of both years. It comprised 48.9 per cent of the 1927 collection and 90.4 per cent of the 1928 collection.

The males and females grow in length at approximately the same rates during the first four years. For some unknown reason it appears that the females of the 1925 year-class grew significantly faster than the males in their third year in the summer of 1927.

The period of most rapid growth in length of the yellow perch is during the first two years (Table III and Fig. 73). During the third year there is a sharp decline in the growth rate. This may be associated with the attainment of sexual maturity. The value of the annual-growth increment decreases somewhat during the fourth year, but at the end of this year a standard length of 197 mm. is reached. This standard length is equivalent to a total length of nine inches, which is the legal limit for perch in several of the Great Lakes states.

The average increase in weight for the age-groups is shown in Table IV and Figure 74.

The data for age-groups IV and V are probably not reliable because of the small number of individuals employed.

ACKNOWLEDGMENTS

I am indebted to Dr. John Van Oosten, in charge of the Great Lakes Fishery Investigations of the United States Bureau of Fisheries, for critical supervision of my work. I am indebted also to Dr. Stillman Wright and Mr. H. J. Deason, both of the United States Bureau of Fisheries, for the collecting of data and materials.

United States Bureau of Fisheries

THE DEVELOPMENT OF THE ELEMENTARY EQUATIONS IN THE THEORY OF DIFFUSION

HUGO KRUEGER

1. INTRODUCTION

GENERAL diffusion equations for particular conditions have been given by different physiologists. Warburg (5) has developed a particular solution of the diffusion equation for a solid bounded by an infinite plane. Krogh (4), Fenn (1), and Gerard (2) have presented special cases of the solid bounded by an infinitely long cylinder. Hill (3) has provided extensive developments and applications of both these cases. The development, so far as the author is aware, of the general diffusion equation is not yet available. Hence it is the object of this paper to offer the development of the general diffusion equation and some of its simpler solutions. A few applications will be indicated.

2. THE GENERAL DIFFERENTIAL EQUATION OF DIFFUSION

It has been found experimentally that, if the concentration of a substance at one of the parallel surfaces of a layer of liquid is w_1, the concentration at the other surface w_2, the thickness of the layer x, and the area of the surfaces A, then the mass of the substance which diffuses through the cross-section A, in time t, is

$$Q = K \frac{(w_1 - w_2)}{x} A\, t, \tag{1}$$

where K is the diffusion constant. It is numerically equal to the quantity of the substance which diffuses in unit time through a unit area of a plate of unit thickness under a unit difference in concentration between the surfaces of the plate.

The limiting value of $\frac{w_1 - w_2}{x}$ is $-\frac{\partial w}{\partial x}$, and represents the concentration gradient or the space rate of change of concentration at any point. Hence equation (1) may be replaced by

$$Q = -K A \frac{\partial w}{\partial x} t, \tag{2}$$

or by the differential form,

$$\frac{\partial Q}{\partial t} = -K A \frac{\partial w}{\partial x}. \tag{3}$$

It is clear from the defining equation that only differences in concentration are involved and that the actual concentrations are immaterial.

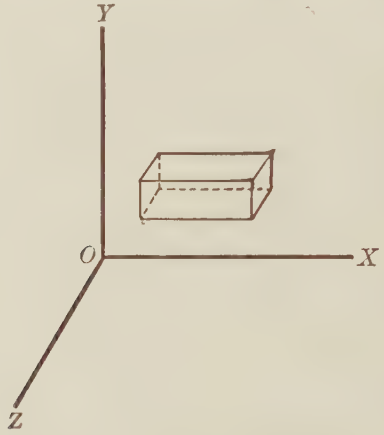

Fig. 75. Rectangular parallelepiped with edges dx, dy, and dz parallel to the x-, y-, and z-axes

Next consider some homogeneous medium in which a substance is diffusing owing to differences in concentration. Take any rectangular parallelepiped with edges $dx, dy,$ and dz parallel respectively to the x-, y-, and z-axes of a rectangular system of coördinates (Fig. 75). Call the concentration at the left-hand $dydz$ face w. The concentration at the right-hand face will be $w + \frac{\partial w}{\partial z} dx$ and the difference in concentration between the two faces will be $\frac{\partial w}{\partial x} dx$. The quantity of material diffusing through the left-hand face in time dt, is

$$\left[\frac{\partial Q}{\partial t} dt\right]_l = -K\, dydz \frac{\partial w}{\partial x} dt, \tag{4}$$

whereas the quantity diffusing through the right-hand face is

$$\left[\frac{\partial Q}{\partial t} dt\right]_r = -K\, dydz \frac{\partial}{\partial x}\left(w + \frac{\partial w}{\partial x} dx\right) dt. \tag{5}$$

The difference between $\left[\frac{\partial Q}{\partial t}\,dt\right]_l$ and $\left[\frac{\partial Q}{\partial t}\,dt\right]_r$ will give the x-component of the change of content of the diffusing substance within the parallelepiped.

$$(6)\quad \left[\frac{\partial Q}{\partial t}\,dt\right]_l - \left[\frac{\partial Q}{\partial t}\,dt\right]_r = -K\,dxdydzdt\,\frac{\partial^2 w}{\partial x^2} = x\text{-component.}$$

Similar expressions hold for the y- and z-components. The total change within the elemental volume, due to diffusion, in the quantity of the diffusing substance, in time dt, is the sum of the x-, y-, and z-components of the change. The total change in the quantity of the diffusing substance in time dt is expressed by $\frac{\partial w}{\partial t}\,dxdydzdt$. Hence, if diffusion alone is involved,

$$(7)\quad \frac{\partial w}{\partial t}\,dxdydzdt = +K\,dxdydzdt\left[\frac{\partial^2 w}{\partial x^2} + \frac{\partial^2 w}{\partial y^2} + \frac{\partial^2 w}{\partial z^2}\right],$$

and

$$(8)\quad \frac{\partial w}{\partial t} = +K\left[\frac{\partial^2 w}{\partial x^2} + \frac{\partial^2 w}{\partial y^2} + \frac{\partial^2 w}{\partial z^2}\right].$$

If the diffusing substance is being formed or removed by chemical reactions, the increased quantity of the substance present in the elemental volume due to the chemical reaction during time dt is $adxdydzdt$, where the factor a is the rate of formation of the substance in a unit volume during a unit time. This quantity must be added to the right-hand member of equation (7) in order to obtain the total increase in the amount of the diffusing substance within the unit volume during time dt. After addition of $adxdydzdt$ to the right-hand member of equation (7) and after the division of all the terms by $dxdydzdt$, we have

$$(9)\quad \frac{\partial w}{\partial t} = +K\left[\frac{\partial^2 w}{\partial x^2} + \frac{\partial^2 w}{\partial y^2} + \frac{\partial^2 w}{\partial z^2}\right] + a.$$

The factor a is positive when the substance is formed, negative when the substance is removed by a chemical reaction.

The last equation, of course, is just a simple modification of the Fourier expression for the conditions determining the flow of heat in a body. The solution of any particular problem in diffusion must satisfy this equation or some modification of it.

3. ONE-DIMENSIONAL DIFFUSION DURING A STEADY STATE

In the problem of the maximum size of a sheet of tissue that would obtain an adequate supply of oxygen it may be considered that all the oxygen enters from the surfaces and none from the edges. If the surfaces are considered as parallel to the yz-plane, the y- and z-components of the diffusion vanish. Hence for this and similar problems equation (9) becomes

$$\frac{\partial w}{\partial t} = K \frac{\partial^2 w}{\partial x^2} + a, \tag{10}$$

and, if it is further assumed that a steady state exists,

$$\frac{\partial^2 w}{\partial x^2} = \frac{-a}{K}. \tag{11}$$

For the specific case of oxygen, since this substance disappears in tissue metabolism,

$$\frac{\partial^2 w}{\partial x^2} = \frac{a}{K}. \tag{12}$$

The general solution of equation (12) is

$$w = \frac{1}{2} \frac{a}{K} w^2 + Bw + w_o. \tag{13}$$

Equation (12) is the equation developed by Warburg (5). Warburg also presented its general solution and, in addition, the particular solution for the determination of the maximum thickness of a sheet of tissue that could be adequately supplied with oxygen. Hill (3) used equation (12) as the starting point for extensive physiological applications.

4. RADIAL DIFFUSION IN A CYLINDER

Some tissues may be treated as long cylinders. If it may be assumed that the component of the diffusion parallel to the axis of the cylinder is zero, equation (9), during a steady state, for a substance destroyed in metabolism, reduces to

$$\frac{\partial^2 w}{\partial x^2} + \frac{\partial^2 w}{\partial y^2} = \frac{a}{K}. \tag{14}$$

Since $x^2 + y^2 = r^2$, $\frac{\partial r}{\partial x} = \frac{x}{r}$ and $\frac{\partial w}{\partial x} = \frac{dw}{dr}\frac{\partial r}{\partial x} = \frac{dw}{dr}\frac{x}{r}$.

Further, $$\frac{\partial^2 w}{\partial x^2} = \frac{d^2w}{dr^2}\cdot\frac{x^2}{r^2} + \frac{dw}{dr}\cdot\frac{1}{r} - \frac{dw}{dr}\frac{x^2}{r^3}.$$

Similar equations hold for y. Hence (14) becomes

$$\frac{d^2w}{dr^2} + \frac{1}{r}\cdot\frac{dw}{dr} = \frac{a}{K}. \tag{15}$$

The general solution of this equation is

$$w = \frac{a}{4K}r^2 + B\log r + E. \tag{16}$$

Equation (16) also has been used by Hill (3) as a starting point for extensive physiological applications. Krogh (4) has presented an equation which is a particular solution of (16).

Hill has developed the equation presented by Krogh somewhat as follows. If a tissue is intersected by capillaries of radius r_o, and each capillary supplies oxygen to a region of tissue of radius r_1, outward diffusion stops at $r = r_1$, and consequently $\frac{dw}{dr} = 0$ at $r = r_1$. The concentration of oxygen at $r = r_o$ is considered as constantly w_o. Then

$$w = \frac{a}{4K}r^2 + B\log r + E,$$

$$w_o = \frac{a}{4K}r_o^2 + B\log r_o + E,$$

$$w = w_o + \frac{a}{4K}(r^2 - r_o^2) + B(\log r - \log r_o),$$

$$\frac{dw}{dr} = \frac{ar_1}{2K} + \frac{B}{r_1} = 0, \text{ at } r = r_1,$$

and

$$w = w_o + \frac{a}{4K}(r^2 - r_o^2) - \frac{ar_1^2}{2K}\log\frac{r}{r_o}. \tag{17}$$

Equation (17) has very important physiological applications. From it the minimum oxygen pressure in the capillaries necessary to supply oxygen to a cylinder of tissue may be computed. If the radius of the cylinder, to which a capillary of radius r_o, supplies oxygen, is r_1, and if the supply of oxygen is just barely sufficient, at $r = r_1$

$$(18) \qquad w = 0 = w_o + \frac{a}{4K}(r_1^2 - r_o^2) - \frac{ar_1^2}{2K} log \frac{r_1}{r_o}.$$

For example, suppose that:

a = oxygen consumption = 0.216 c. c. per gram per minute;

K = diffusion constant of oxygen = 1.64×10^{-5} c. c. per sq. cm. per minute under a diffusion gradient of one atmosphere per minute (Krogh);

r_1 = 0.00248 cm.;

r_o = 0.0003 cm.;

then

$$w_o = -\frac{0.216 \times (24.8^2 - 3^2) \times 10^{-8}}{4 \times 1.64 \times 10^{-5}} + \frac{0.216 \times 24.8^2 \times 10^{-8}}{2 \times 1.64 \times 10^{-5}} log_e \frac{24.8}{3}.$$

w_o = 0.0658 atmospheres = 50 mm. Hg.

The value of w_o will be expressed in atmospheres. It may be reduced to mm. Hg. by multiplying by 760. Though the equations have been developed for concentration, in the case of gases pressure or tension may be substituted for concentration by use of the proper solubility coefficient.

If the oxygen pressure available should be only 30 mm. Hg., it is obvious that some of the tissue would not receive oxygen. The radius of the portion receiving oxygen would be given by

$$\frac{30}{760} = \frac{-0.216 \times (r_1^2 - 3^2) \times 10^{-8}}{4 \times 1.64 \times 10^{-5}} + \frac{0.216 \times r_1^2 \times 10^{-8}}{2 \times 1.64 \times 10^{-5}} log_e \frac{r_1}{3}.$$

r_1 = 0.00205 cm. = 20.5 μ.

A slightly different type of problem is met in the diffusion of lactic acid. This substance may diffuse toward or away from the capillaries, depending upon specific conditions. If the diffusion is toward the capillaries, the quantity a of equation (7) becomes

negative. If the concentration of lactic acid is maintained at a constant level w_o in the capillaries, and if the rate of formation of lactic acid has the magnitude a,

$$w = \frac{-a}{4K} r^2 + B \log r + E,$$

$$w_o = \frac{-a}{4K} r_o^2 + B \log r_o + E,$$

and

$$w - w_o = \frac{-a}{4K} (r^2 - r_o^2) + B \log \frac{r}{r_o}.$$

If each capillary is considered to drain a specific region bounded by a cylindrical surface of radius r_1 (through the medium of an impermeable membrane at $r = r_1$ or through some other device), then $\frac{\partial w}{\partial r} = 0$ at $r = r_1$ and

$$\frac{-a}{4K} 2r_1 + \frac{B}{r_1} = 0.$$

Finally,

$$w - w_o = \frac{a}{4K} (r_o^2 - r^2) + \frac{a}{2K} r_1^2 \log \frac{r}{r_o}. \tag{19}$$

Here w is the concentration at any point r; w_o is the concentration maintained at r_o; K is the diffusion constant of lactic acid; a is the rate of formation of lactic acid; r_o is the radius of the capillary; and r_1 is the radius of the region drained by the capillary.

If we are interested in the radial diffusion of a substance whose concentration undergoes no changes due to formation or removal by a chemical reaction, the constant a in equation (7) vanishes, and, during a steady state,

$$\frac{d^2w}{dr^2} + \frac{1}{r} \frac{dw}{dr} = 0.$$

The solution of this equation is

$$w = C \log r + B.$$

If a concentration w_1 is maintained at r_1, and a concentration w_2 at r_2,

$$w_1 = C \log r_1 + B,$$
$$w_2 = C \log r_2 + B,$$
$$C = \frac{w_1 - w_2}{\log r_1 - \log r_2},$$
$$B = w_1 - \frac{(w_1 - w_2) \log r_1}{\log r_1 - \log r_2} = \frac{w_2 \log r_1 - w_1 \log r_2}{\log r_1 - \log r_2},$$

and

$$w = \frac{(w_1 - w_2) \log r + (w_2 \log r_1 - w_1 \log r_2)}{\log r_1 - \log r_2}. \tag{20}$$

The rate of flow in the direction r across unit area in unit time is given by

$$F = -K \frac{dw}{dr} = \frac{-K (w_1 - w_2)}{r (\log r_1 - \log r_2)}, \tag{21}$$

and the total quantity that will diffuse from r_1 to r_2 through a unit length of cylinder in unit time by

$$T = 2\pi r F = \frac{2\pi K (w_1 - w_2)}{\log r_2 - \log r_1}. \tag{22}$$

5. DIFFUSION INTO OR OUT OF A SPHERE

If the concentration of any substance is maintained constant over the entire surface of a sphere, the concentration at any point, during a steady state, is a function of the radius only. Here $r^2 = x^2 + y^2 + z^2$ and the partial derivatives with respect to x, y, and z undergo the transformations indicated under equation (15). Hence equation (9) is transformed to

$$\frac{d^2w}{dr^2} + \frac{2}{r}\frac{dw}{dr} = \frac{a}{K}, \tag{23}$$

for substances disappearing in metabolism.

The general solution of this equation is

$$w = \frac{a}{6K} r^2 + \frac{B}{r} + C. \tag{24}$$

If oxygen penetrates the entire sphere, since the concentration throughout is finite, $B = 0$. For otherwise the concentration at $r = 0$ becomes infinite.

If the concentration is w_o at the boundary r_o,

$$w_o = \frac{a}{6K} r_o + C \text{ and } C = w_o - \frac{a}{6K} r_o^2.$$

Substituting these values of B and C in equation (24) we have

$$w = \frac{a}{6K} (r^2 - r_o^2) + w_o. \tag{25}$$

The concentration at $r = 0$ is

$$w = w_o - \frac{a}{6K} r_o^2.$$

If $w = 0$, when $r = 0$, i.e. the limiting condition for maximum oxidations without the development of an oxygen debt,

$$w_o - \frac{a}{6K} r_o^2 = 0, \tag{26}$$

and

$$r_o = \sqrt{\frac{6K w_o}{a}}. \tag{27}$$

Hence the maximum or critical radius of a successful spherical cell is inversely proportional to the square root of its rate of oxygen consumption and directly proportional to the square root of the concentration of oxygen maintained at its boundary.

If oxygen does not penetrate the entire sphere, the solution of equation (24) will be somewhat different. If inward diffusion stops at $r = r_1$,

$$w = \frac{a}{6K} r^2 + \frac{B}{r} + C;$$

$$w_o = \frac{a}{6K} r_o^2 + \frac{B}{r_o} + C.$$

At $r = r_1$,

$$\frac{dw}{dr} = \frac{a}{3K} r_1 - \frac{B}{r_1^2} = 0,$$

and

$$w = w_o + \frac{a}{6K} (r^2 - r_o^2) + \frac{a}{3K} r_1^3 \left(\frac{1}{r} - \frac{1}{r_o}\right). \tag{28}$$

If the diffusing substance is being formed throughout the cell at a constant rate, and if a constant concentration is maintained at the border of the cell,

$$w = \frac{-a}{6K} r^2 + \frac{B}{r} + C;$$

$$w_o = \frac{-a}{6K} r_o^2 + \frac{B}{r_o} + C.$$

$$w = w_o - \frac{a}{6K} (r^2 - r_o^2). \tag{29}$$

The quantity of diffusing substance within the cell will be

$$\begin{aligned} Q &= \int_o^{r_o} 4\pi r^2 w dr \\ &= 4\pi \int_o^{r_o} r^2 \left[w_o - \frac{a}{6K} (r^2 - r_o^2) \right] dr \\ &= \frac{4\pi}{3} r_o^3 w_o + \frac{a}{6K} \cdot \frac{8}{15} \pi r_o^5, \end{aligned} \tag{30}$$

and the average concentration of the diffusing substance will be

$$\bar{y} = \frac{Q}{V} = w_o + \frac{1}{15} \frac{a}{K} r_o^2. \tag{31}$$

By means of the equations given above, the concentrations and variations in concentrations of some materials, as they occur throughout the tissues, can be computed from the available biological data. An approximation only will be obtained, however, since many simplifying assumptions have to be made in the application of these equations to data from biological systems.

The author hopes to present some physiological applications of the foregoing equations in a future paper. He wishes to thank Dr. V. C. Poor and Dr. R. L. Wilder of the Mathematics Department for their friendly advice.

University of Michigan

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CONTRIBUTION TO THE BIOLOGY OF FRESH-WATER SPONGES (SPONGILLIDAE) *

MARCUS C. OLD

I. Field Observations on Growth

THE literature on fresh-water sponges contains statements that they disintegrate with the onset of unfavorable conditions in the fall and that they then liberate their gemmules, which are spread by slowly sinking or drifting to new places. Thus any growth would be of one season only. These statements are badly in need of verification, since they appear to be largely inferential. The investigation described below was carried out in an attempt to extend our knowledge of seasonal growth.

METHODS

Bessey Creek, Douglas Lake, Michigan, contains many colonies of sponges which are unusually large during the summer season. This habitat seemed a good one in which to find out whether these sponges represent one season's growth, and if not, how much is the growth of a single season. Since many colonies are spindle-shaped, coating slender twigs and branches, measurements of maximum length and thickness were easily made, and a marker for the sponge was attached. Each marker consisted of a small square of sheet copper on which was stamped a letter or number. Two lengths of copper wire fastened to the sides of the marker were then tightly wound around the branch, or other supporting object, exactly at the ends of the sponge. During three

* Contribution from the Biological Station and the Zoölogical Laboratory of the University of Michigan.

successive years sponges were marked in the fall and recovered the following summer.

RESULTS

Tables I and II give the data on experiments made in Bessey Creek during the period from 1926 to 1929. All the sponges tagged were identified on recovery as *Ephydatia mülleri* (Lieberkühn).

On June 27, 1929, a specimen of *Spongilla fragilis* Leidy, twenty-four inches in total length and three inches in its greatest width, was found in a small, shallow, temporary pond near Ann Arbor, Michigan. It was a beautiful green specimen, which coated a fallen twig and rested on the bottom of the pond in about twelve inches of water. Closer examination revealed that the living part was really only one-eighth to one-half inch thick; the remaining part consisted of dark, dead tissues that contained very many gemmules. The specimen evidently remained intact and grew larger each year by accretions on the old body. In August of 1929 this pond became totally dry; it accumulated waters again by the latter part of October and was frozen during the winter. On March 27, 1930, growing sponges were again found in the pond.

DISCUSSION

The condition of the colonies when retrieved, together with the fact that many were lost, suggests that Bessey Creek is subject to severe ice action. Only approximately 60 per cent of the sponges tagged were recovered, and of these many were in a ragged, broken condition, and with over all dimensions smaller than when tagged. There were a few, however, that had escaped injury and showed a decided increase in size by the following year. Apparently, *E. mülleri* may remain intact and build anew on the old structure as soon as conditions permit. Figure 76 is a photograph of a specimen tagged in August, 1927, and recovered in August, 1928. The increase in size during the favorable season was at least 13 cm. in length and 4.5 cm. in total thickness. *S. fragilis* apparently also remains intact and increases in size each year by growths on the surface of the old body.

VOLUME OF NEW GROWTH

A notion of the volume of new growth each season may be computed by assuming a spindle-shaped colony to approximate the volume of two similar cones placed base to base. Then the

FIG. 76. Sponge A of Table I, tagged on August 16, 1927

volume of a sponge on one date less the volume of the same sponge on a preceding date gives the volume of new growth during the interval. From the computations it may be seen that sponge A, for example, had on August 16, 1927, a volume of 176.9 c. c.; on June 22, 1928, of 158.3 c. c.; and on August 10, 1928, of 918.6 c. c.

TABLE I

I. Sponges Tagged on August 10, 1926

No.	Measurements when tagged	Date recovered	Measurements at recovery	Growth
5	42 cm. × 2 cm.*	.....	.....	.....
6	29 cm. × 9 cm.	Aug. 11, 1927	44 cm. × 16 cm.	15 cm. in length 7 cm. in width
7	9 cm. × 4 cm.*	.....	.....	.....
8	22.5 cm. × 4.5 cm.	do.	35 cm. × 13 cm.	12.5 cm. in length 8.5 cm. in width
9	23 cm. × 4.5 cm.*	.....	.....	.....
10	23 cm. × 5 cm.	do.	25.5 cm. × 6.5 cm.	2.5 cm. in length 1.5 cm. in width
11	9 cm. × 6 cm.*	.....	.....	.....

II. Sponges Tagged on August 16, 1927

A	16 cm. × 6.5 cm.	June 22, 1928	20 cm. × 5.5 cm.	4 cm. in length Lost 1 cm. in width
		Aug. 10, 1928	29 cm. × 11 cm.	13 cm. in length 5.5 cm. in width
B	26 cm. × 6.5 cm.*	.....	.....	.....
C	21 cm. × 3.5 cm.	June 22, 1928	21 cm. × 2 cm.	Lost 1.5 cm. in width
		Aug. 10, 1928	29 cm. × 3.5 cm.	8 cm. in length 1.5 cm. in width
D	6.5 cm. × 4 cm.*	.....	.....	.....
E	18 cm. × 6 cm.	do.	10 cm. × 2 cm.	Lost 4 cm. in width, 8 cm. in length. Original body broken up during winter

* Specimen lost.

Therefore, sponge A lost approximately 18.6 c. c. during the winter, but during the next favorable season it formed 760.3 c. c. of new growth, practically four times the original volume. By the same method it is found that sponge 6 of Table I had on August 10, 1926, a volume of 614.9 c. c., and on August 11, 1927, 2,948.9 c. c., or a gain of over 2,300 c. c.

Any such computation was applicable only in situations sim-

TABLE II

SPONGES TAGGED ON OCTOBER 27, 1928

No.	Measurements when tagged	Date recovered	Measurements at recovery	Condition of sponge at recovery
1	38 cm. × 9 cm.*	.....	.....	.....
2	49 cm. × 9 cm.	June 22, 1929	43 cm. × 5 cm.	Old colony dark brown; three green patches, 1 cm. sq., on surface
3	23 cm. × 4 cm.	do.	.....	Only traces of old colony left; branch nearly broken away
4	38 cm. × 2.5 cm.	do.	.....	Only traces of old colony left
8	28 cm. × 10 cm.	do.	.....	Like No. 3
9	15 cm. × 11 cm.	do.	15 cm. × 5 cm.	Covered with silt and slime; broken up
10	15 cm. × 8 cm.	do.	.....	Like No. 3; several patches of green growing on surface; branch broken off, but still clinging by wire to original stem
11	13 cm. × 4 cm.	do.	.....	Like No. 9; several green growths on surface
12	25 cm. × 9 cm.	do.	.....	Like No. 11
13	23 cm. × 6 cm.*	.....	.....	.....
16	30 cm. × 8 cm.	do.	.....	Like No. 11
17	11 cm. × 3 cm.	do.	.....	Nothing left of old colony between wires
18	23 cm., flat type	do.	.....	Few irregular broken patches of old colony remaining
		Aug. 21, 1929	20 cm. × 2.5 cm.	Lost 3 cm. in diameter, but gained in thickness
21	8 cm., flat type	June 22, 1929	.....	Only marker recovered
22	10 cm., flat type	do.	.....	Only traces of old colony left; covered with silt and slime
23	19 cm. × 7 cm.	do.	.....	Broken up; found on bottom of stream

* Specimen lost.

ilar to those in Bessey Creek, where the numerous colonies almost invariably grew on fairly slender limbs of small trees whose tops had fallen into the water. On these slender supports the general tendency of the colony was to assume the form referred to above,

particularly after it had become large enough to encircle the limb completely. Colonies thus approximate the spindle shape, with the greatest thickness at the middle, and a thinning off toward the extremities. Obviously a different method of arriving at a measure of increase in volume would have to be used for sponge colonies of other forms.

Although the experiments described above and one field observation are not wholly conclusive, they suggest the following probabilities: (1) that sponges inherently remain intact, if possible, during unfavorable conditions and build anew upon and among the old structure to form larger colonies, the size of which depends on the base of attachment, i.e. a thin twig can carry only a certain weight, but a larger support allows development of a larger sponge; (2) that sponge bodies normally die at the close of the favorable season after producing gemmules to assure reproduction at the renewal of favorable conditions; (3) that summer growth begins immediately after the renewal of favorable conditions, as it did, for example, in a pond near Ann Arbor as early as the last week in March; and (4) that this growth in one season may exceed 2,500 c. c.

GEMMULE SPICULES IN IMMATURE FORMS

Sponges collected during the early summer months may not show gemmules, but often in the making of slide preparations for the various kinds of body spicules gemmule spicules are also encountered. The writer believes that their presence may be explained by results of the experiments in yearly growth. Since the sponge body may remain intact, if external conditions permit, the gemmules are not liberated and, even after germination, parts, at least, of the gemmules must remain in the body and so account for gemmule spicules. Accidental inclusion of old gemmules liberated upstream from other sponges is not probable for two reasons: (1) unless the stream is a fairly swift one, the gemmules sink to the bottom, being weighted down by the siliceous spicules; (2) even if such a thing should happen, one would also expect to find gemmule spicules of different species, or at least some gemmule spicules that do not fit in with the other

spicules of the sponge in question. Such spicules were never found.

PERENNIAL GROWTH

It is known that some sponges do not necessarily die at the approach of winter. Potts (1887) has found green, growing specimens of *S. aspinosa* throughout the winter; Crowell (1926) reports *Heteromeyenia ryderi* in ice-covered streams; and the writer has often collected *S. lacustris* at depths of from three to six feet in Third Sister Lake, near Ann Arbor, Michigan, during the winter season. Nearer the shore and at shallower depths the same species became abundantly filled with gemmules in the fall and died. Occasional sponges found growing during the winter have possessed gemmules, and one specimen of *H. ryderi*, collected by Crowell, had gemmules. So far, the belief has been that none of these "evergreen" sponges form gemmules, but that they modify themselves otherwise to withstand the low temperatures. According to Weltner (1893), Lieberkühn has reported the absence of flagellated chambers, Metschnikoff found no canals, and Wierzejski found neither canals nor flagellated chambers in *E. fluviatilis* in the winter. Weltner repeated the work and found flagellated chambers and canals, but restricted in size in the winter, which suggested a dormant condition. Wierzejski believed it to be an embryonic condition similar to that of the gemmule content. Though the writer has nothing to add to our knowledge of these anatomical conditions during the winter, there are two facts which present themselves: (1) sponges which normally form gemmules may nevertheless, on occasion, become perennial; (2) even sponges having regularly formed gemmules apparently may continue to live through the winter.

REPRODUCTION DURING THE SUMMER

Thousands of small colonies of sponges, varying from one-half to five mm. in diameter, living on the recent growths of submerged vegetation, were found in Bessey Creek by Professor Paul S. Welch on August 17, 1926. The writer has never witnessed a case like that, but he has collected in different waters where similar small sponges occurred in large numbers together with

sponge colonies which were of a large size and possessed gemmules. It could not be definitely shown whether these small sponges were the result of that season's crop of gemmules or of sexual reproduction. Though sexual reproduction is generally supposed to take place at the beginning of the favorable season, it nevertheless appears from general considerations that these small sponges may be due to fertilized ova. Their abundance and their uniformly small size suggest a haphazard settling of the free-swimming sponge larvae.

II. Associated Macroörganisms

The microörganisms and the macroörganisms associated with fresh-water sponges have received attention from many writers, among whom are Annandale (1907, 1911, 1916), Lieberkühn (1856), Needham (1901), Stebbing (1907), Stephenson (1910), Viets (1927), and Weltner (1894). In conjunction with various studies on fresh-water sponges the writer collected whatever macroörganisms were on or in the sponge.

The organisms were as follows: larvae of Chironomidae, Dytiscidae, Ephemeridae, Odonata, Simuliidae, Sisyridae, and Trichoptera; Amphipoda; Bryozoa; Gordiidae; Hirudinea; Hydracarina; Isopoda; Mollusca; Nematoda; and Oligochaeta. With the exception of *Gordius*, all have been previously reported. This specimen of *Gordius* was found entwined in and about the base of a branched colony of *S. lacustris* in a narrow, shallow stream. Its presence, as may also be true of all except the Sisyridae, was probably accidental. Certain forms, such as Trichoptera and chironomid larvae, occur in very frequent association with the sponge, and it seems that these forms may actually seek the sponges. In Third Sister Lake one sponge, *S. lacustris*, yielded various stages of the water mite from the egg to an adult, which was identified by Professor Ruth Marshall as *Unionicola crassipes* (Müll.). It is believed that this common hydrachnid may be parasitic on sponges.

No study has been made of the relationships of the various species to sponges, but it appears that the list of forms found represents a somewhat graded series from the purely accidental

to the completely necessary. There are those, such as the sisyrids, which have an inseparable relation with sponges; others, such as the caddis fly and chironomid larvae, oligochaetes, nematodes, etc., may find at least a retreat in the sponge body, and it is not wholly inconceivable that they may find in it accumulations of food materials. If the sponge acts as a screen, sifting material out of the water with consequent accumulation within the surface irregularities, why should not animals discover and take advantage of it?

It is also likely that insects may aid in the dissemination of sponges, at least from one part of a continuous body of water to another. This has already been mentioned by Krecker (1920), who found that the parchment-like cases of caddis worms in Lake Erie were encrusted with small sponges. The writer has also noticed this condition in sponges from a lake and a pond near Ann Arbor, where caddis worms which have cases of the log-cabin type were encrusted with sponges, as were also the parchment cases.

III. Culture Experiments

No one has ever reared fresh-water sponges under laboratory conditions. Sponges allowed to remain a few days in unreplenished water quickly become foul, release a most offensive odor, and disintegrate. Renewal of the water only delays disintegration.

Potts (1887), Brocher (1913), and Van Trigt (1919) have devised methods by which sponges have been kept for several months in aquaria. The containers varied from small vessels of one-liter capacity to larger vessels of one hundred liters, and the water was renewed either continuously by tap or at intervals of a day or two. Van Trigt was able to keep *Spongilla* in this fashion from one to one and one-half months, and *Ephydatia* usually lasted five months.

For true laboratory culture, sponges must not merely exist for several months but actually thrive for periods sufficiently long to duplicate their existence in nature and to reproduce. With experimental facilities and ample materials at hand, the writer undertook the solution of this puzzling problem of sponge-culture.

As will be shown, all the attempts were negative. Nevertheless, the methods and the results are presented, since they may contribute to the construction of new methods for a future attack. It is highly desirable, from many standpoints, to discover the explanation for true laboratory culture of fresh-water sponges.

Observation and Results

During the summers of 1926 and 1927 several experiments were made at the Biological Station of the University of Michigan, Douglas Lake, Michigan. The facilities included a pump and giant storage tanks, which furnished a continuous supply of unmodified lake water for the aquaria. Presumably this water was suitable in all respects, since sponges grow in certain parts of the lake. In the laboratories of the Department of Zoölogy, University of Michigan, culture experiments were continued during the period from 1926 to 1929.

Experiment 1. — Three glass aquaria, $10\frac{1}{2} \times 12 \times 18$ inches, filled with lake water, were arranged in line and connected with one another by glass siphons, so that the water of one aquarium flowed over into the next. All aquarium bottoms were covered with sand in which were anchored a few common water plants. The set-up stood under a shelter on the east side at an open window considerably shaded by trees. After lake water had been running through the aquaria five days, sponges were added and notes taken daily on their general appearance. Limnological analyses show that the water of Bessey Creek near its mouth is very similar to that of Douglas Lake, into which it flows. It may be noted also that a few sponges have been found in that part of the lake. The sponges used varied from spindle-shaped colonies, 3×1 inches, to flat, subcircular colonies, one-eighth inch in diameter. Some were green, others a pale brown. The object of attachment may have been gravel, wood, branches, or vegetation.

At the end of eight to fourteen days the colonies presented a thin, emaciated, spinose condition. The green sponges became covered with heavy growths of filamentous algae, which could be washed off, but in any case the sponges became paler and finally

white. The non-green sponges developed no filamentous growths, but deteriorated similarly and became white; a few became moldy. At no time was any offensive odor noticeable; the odor was always that of the fresh sponge, but not so strong.

Experiment 2. — To make certain that collection and transportation of sponges from the field to the laboratory was not at fault, three sponges were taken out of Bessey Creek, put into a galvanized iron pail, carried around with deliberate carelessness for thirty minutes, and then left standing in direct sunlight for forty more minutes. After this treatment they were returned to their original resting place in the creek and tagged. Fifteen days later examination showed them to be as healthy as they had been before the treatment. Evidently proper transportation has little, if any, effect.

Experiment 3. — A second set-up was made in the same spot as that of Experiment 1. Two aquaria with sand bottoms each received a continuous supply of unmodified lake water by separate inlets at the rate of four gallons per hour, with excess water leaving at the surface. On July 7, 1927, two small green sponges were placed in each aquarium to test the effect of an abundant water supply. On July 16, 1927, they were still green, but had lost their porous character. The odor was that of a fresh specimen. On July 26, 1927, the sponges were very much emaciated; one was covered by a mold.

Experiment 4. — The inlet tubes of two aquaria were provided with a Y-tube, one arm of which, being left open, allowed air to be carried into them with the unmodified lake water. Sponges fared no better in these aquaria; one spindle-shaped colony coating a slender branch became so emaciated by the end of sixteen days that it slipped along the branch to the bottom. Other sponges inserted at different times retained a healthy aspect from seven to sixteen days.

Experiment 5. — Since these aquaria stood in a shaded place, another one was set up outside the shelter, where it received subdued sunlight from noon to sunset. Otherwise the conditions were identical with those of the previous experiment. On July 19, 1927, two spindle-shaped green colonies, $3\frac{1}{2} \times 9$ inches and

$\frac{3}{4} \times 3$ inches, were placed in it. These sponges seemed to fare better; not until three weeks later was there an appreciable difference in color. With this change the surface developed a sort of velvety smoothness, with loss of porous nature. A few days later, however, the sponges were thin and scraggy, and the sides of the aquarium became lined with slimy green patches.

Experiment 6. — This set-up consisted of six aquaria with gravel bottoms, in which circulation of water was accomplished by allowing compressed air to accumulate in the large end of inverted glass funnels in one aquarium, and thus force the water over into other aquaria. It returned to the first aquarium by way of siphons. Lake water was used exclusively. This automatically provided the proper food materials as well as the proper kind of water. Branched colonies of *S. lacustris* were introduced after the water in the aquaria had been running for four days, but the sponges lapsed into pale, deteriorating bodies in from three to ten days. Experiments were run over a period of two months; in all, the results were similar.

Experiment 7. — Since Potts (1887) found that gemmules germinated and grew for some time in a glass bowl containing only tap water, it was decided to attempt an experiment with tap water only. With the set-up of the previous experiment, and tap water instead of lake water, another series of colonies of *S. lacustris*, together with *E. mülleri*, were observed over a period of six months. Again the healthy sponge degenerated into a fragile body of spicules.

Experiment 8. — Two aquaria were set up with four-inch, six-paddle wheels. One wheel was placed so that about two thirds of it was out of the water. The wheel was revolved by a jet of compressed air against the upper blades, which in turn imparted a movement to the water. By regulating the force of the jet of air and the consequent speed of the wheel the water could be made to rotate more slowly, or faster. Another wheel was placed near the bottom of the aquarium at the middle of one end; air bubbles rising from a tube properly placed made the wheel revolve and gave to the water a motion that was both upward and downward, as well as rotation. Lake water was added every

three or four days. The purpose of the paddle wheels was to cause a movement of the water, which served to duplicate, in a way, the movement of water in a stream and to bring any food materials in the water within closer reach of the sponges. Observations over eight weeks on sponges added periodically yielded negative results; the sponges lasted only from four to eight days.

Experiment 9. — One large aquarium, 14 × 15 × 25 inches, was filled with tap water and continually aërated. Additions of lake water were made at intervals of from three to four days. Five goldfish were also transferred to this aquarium and fed, twice a week, with a carbohydrate-protein preparation. Specimens of *S. lacustris*, which had been collected in the fall and which had already formed a few gemmules, continued to form them in the aquarium. Some filaments became filled with gemmules; others had few or none. A few specimens which had no indications of gemmules when brought to the laboratory developed some in five to ten days. In the latter case, however, the gemmules were very small, possessed no spicules, and were wont to germinate only after about five months; they produced small green patches that persisted for only three to ten days. Normal gemmules, either those brought in as such from the lake or those formed in the aquarium, remained inactive from two to four months, after which they germinated. When placed in the aquarium most of the gemmules began to germinate about two months after being collected, and continued a slow growth from six to seven weeks. Some of the growths, one-sixteenth to one-eighth inch in diameter, occasionally coalesced to form a green mass, $1\frac{1}{2} \times \frac{1}{8}$ inches, after which the mass gradually disappeared. Others produced a few naked gemmules, which in turn germinated in about ten days and then disappeared.

Experiment 10. — Portions of *S. lacustris* bearing gemmules were brought to the laboratory in October and kept in finger bowls in constantly aërated lake water. In the following February twelve pieces of this sponge, containing numerous gemmules, were transferred to tall, narrow glass vessels filled with tap water and set outside the laboratory window, where they remained until April. During this time the water froze and thawed ten times. Five

days after the specimens had been brought inside, gemmules of six pieces showed signs of germinating and were removed to constantly aërated tap water. This tap water received additions of lake water and the carbohydrate-protein preparation for the goldfish. Thirty-one days later all signs of sponge life had disappeared, and the sides of the aquarium were covered with slimy brown patches.

Experiment 11. — Gemmules which had been gathered in the fall and which had been kept in aquaria at temperatures above freezing were placed in watch glasses to find out whether they would germinate without subjecting them to freezing temperatures. They were placed in watch glasses, one to five in a glass, containing tap water, lake water, or distilled water. To prevent evaporation one set of eight glasses was covered with extra glasses. Another set of eight was left open. Thirteen days later all gemmules of the first set had begun to germinate, and gradually increased in size, forming a body, one-fourth to one-half inch in diameter. The gemmules germinated and grew equally well in tap water, lake, or distilled water. Food was supplied from three to five days after germination by adding fresh lake water to some, organic débris and soil to others, and protozoan cultures to still others. In all cases, after the eighth day, the sponges grew pale and deteriorated, occasionally becoming moldy. Dishes not covered had to have water added daily, owing to the loss by evaporation. These gemmules did not germinate until twenty days later. Two days after this time they were placed in aquaria, but they deteriorated in from five to eight days.

DISCUSSION

All the results of the sponge-culture experiments are negative. Growing sponges or their internal buds apparently continue their biological activities for a few weeks, but can survive the artificial environment for only a few days. Failure does not appear to be due to lack of food, since it was furnished by the water from the original habitat, or by organic débris and soil from the same source. Oxygen requirements were met by continual aëration. The pH of 8.0 to 8.2 is within their range of tolerance as they have been

found in natural habitats in Michigan by the writer. The water was circulated to aid them in obtaining their necessities in it.

In the shallow, natural bodies of water gemmules may be frozen for some time. Potts (1887) grew *S. lacustris* from gemmules frozen during the winter. Weltner (1893) found in laboratory experiments that freezing did not, in general, affect the germinative power of gemmules. During experiments lasting two months the writer was able to germinate gemmules that had frozen and thawed ten times in periods that averaged three days. This indicates that in nature freezing, at least encasement in ice, is not necessarily fatal to gemmules. There are zoölogists who believe that gemmules *must* undergo freezing before they germinate. This is not the true case, since gemmules protected from freezing also germinated.

In all parts of the world gemmules undergo a quiescent period before germinating. This period corresponds to the dry period of the tropics or the winter period of the temperate and arctic countries. It has been inferred in the literature that a quiescent period is necessary before gemmules are able to germinate. The experiments of the writer also seem to confirm this notion, for conditions, at least so far as temperature was concerned, were favorable, yet no germination occurred until a minimum of two months later. Abnormal gemmules formed in the aquaria rested only fifteen days before germinating.

Since cultural experiments were done by the writer in advance of the environmental work, there was no chance to make use of the information accumulated on optimum sponge habitats (Old, 1932). However, from the observations made on more than one hundred natural habitats in Michigan, the author, at the present time, would not attempt further experiments with ordinary small glass aquaria, but would substitute larger shallow basins with such accessories as would tend to duplicate natural conditions more fully. Fine specimens of sponges were found in shallow streams or connecting waters that were but one and one-half to three feet wide, as well as in the larger streams. Sponges were found in small shallow ponds also, but most of them were quite small and produced gemmules apparently earlier than did the

sponges in larger bodies of water. Early production of gemmules, together with small body size, suggests a habitat that is unfavorable. The better arrangement, then, would be to try to duplicate factors of flowing waters. Probably a shallow, long basin or trough with an abundant, continuous supply of water containing food organisms or materials would solve the problem.

SUMMARY

1. Fresh-water sponges tend to remain intact during the winter, and build anew the following spring upon and within the old structure.

2. A list of associated macroörganisms is presented, with suggestions concerning the relationships, purely accidental to obligate, between them and sponges.

3. Gemmules appear to withstand freezing, and alternate freezing and thawing. Further evidence that gemmules require a quiescent period before germinating is presented.

4. The continuous culture of fresh-water sponges is still an unsolved problem.

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Ursinus College
Collegeville, Pennsylvania

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OBSERVATIONS ON THE SISYRIDAE (NEUROPTERA) *

MARCUS C. OLD

IN THIS country the only contribution to the general biology of the spongilla flies or Sisyridae has been made by Needham and Betten.[1] Their life-histories are not known, since attempts to rear them have been unsuccessful, owing to the fact that they are dependent upon living fresh-water sponges. A few observations on larvae, pupae, and imagoes were made by Needham, who found them on sponges growing in water-supply troughs in a fish hatchery.

During the summers of 1926, 1927, and 1928 at the Biological Station of the University of Michigan, Douglas Lake, Michigan, the writer collected many larvae of Sisyridae, which he transferred to the laboratory in order to continue observations on their activities. They were placed in finger bowls containing water, a thin layer of sand, and a pebble large enough to extend above the water. Pieces of fresh sponge replaced old pieces every day. The larvae sometimes fed on the sponge, sometimes not. Often they showed no evidence of even being aware of its presence. Thirty-eight larvae, distributed in ten finger bowls, varying in size from 0.5 to 4.0 mm., were treated thus. About 60 per cent of them died within two to ten days. Of the remaining 40 per cent which pupated, 80 per cent emerged in from eleven to fifteen days. At pupation the larvae had a length of 3.5 to 4.0 mm.

* Contribution from the Biological Station and the Zoölogical Laboratory of the University of Michigan.

[1] Needham, J. G., and Betten, C., "Aquatic Insects in the Adirondacks," *Bull. New York State Mus.*, No. 47. 1901.

Immediately before pupating the larvae walked excitedly over the exposed surface of the pebble, now hurriedly and then feebly, for forty-five to seventy-five minutes. Having finally selected a site, usually a small notch or angle, they would wave their antennae and at the same time indulge in telescopic movements of the abdominal segments. Some would spin hemispherical nets over themselves before forming their cocoons; others would make the cocoons without first enclosing themselves in silken cages. According to Needham, only *Climacia* builds the hemispherical net.

The purpose of this loosely woven net is not known. It might serve as a protection from certain parasitic insects. It does not, however, protect the pupa from becoming wet during submergence, as was shown by experiment.

A larva swims about by a peculiar body movement. It holds itself in a vertical position, head up, arches the body, and then,

Fig. 77. Swimming movements of larvae of Sisyridae

by snapping back into the vertical position, produces a forward movement. See Figure 77.

During the summer of 1927 many pupae and larvae were collected at the mouth of Maple River, Burt Lake, south of Douglas Lake. Field trips to this locality yielded more than five hundred pupae, some of which contained parasitic Hymenoptera. Both *Sisyra* and *Climacia* cocoons occurred in abundance on Scirpus culms at rough spots or in the spikelets. Many were found alongside gyrinid cocoons on these same stems. Groups of from four to eight cocoons, side by side, were common. Cocoons were also found in exposed snags. Many larvae were just coming out of the water and walking up the Scirpus stems. These, when brought to the laboratory and placed in vials, immediately pupated, and emerged in from eight to fourteen days.

In Nigger Creek, near Mullet Lake, which is southeast of Douglas Lake, many sisyrid cocoons were found on the under side of stones above water. Stones partly in the water, but with their under sides concave and forming a small chamber above water, also yielded numerous cocoons.

Pupae brought into the laboratory emerged and afforded material for experiments on life-history. Twenty-five cocoons were placed in a natural position over an aquarium containing sponges and water plants, the latter projecting above the surface of the water. A cage of cloth netting was adjusted over the aquarium. As the imagoes emerged, they flew to the top of the cage, sought a secluded corner, and remained there, rarely flying about. From three to five days later the flies could be picked from the surface of the water, where they had fallen. They appeared very weak in flight, and the slightest wetting rendered them unable to extricate themselves. Examination of the water and plants revealed no evidence of eggs. Repeated observations yielded no results. Flashing a light on imagoes at night caused them to fly about toward the light and exhibit positive phototropism.

During the collection of sponges throughout the State of Michigan in 1929 the writer found many sisyrid larvae. They were recovered from sponges in habitats whose pH varies from 6.2 to 8.5. They were not found on the following species of fresh-water sponges: *Ephydatia fluviatilis*, *Heteromeyenia repens*, and *H. argyrosperma*. This suggests that Sisyridae may be found to show a specificity for certain species of sponges. Absence of larvae in *H. repens* and *H. argyrosperma* may be due to the fact that so few specimens of these species were collected, but, on the other hand, it should be pointed out that quantities of *E. fluviatilis*, without any larvae, were found at various points in the Grand River, a polluted stream, near Lansing. It remains uncertain, however, whether the absence of larvae in the Grand River is due to a difference in the sponge or to contamination. Five other collections of *fluviatilis* from uncontaminated waters showed this same absence of larvae.

It is not possible at the present time to identify with certainty

the different species of sisyrid larvae, hence nothing can be stated concerning the relation of different species of larvae to different species of sponges. Intensive work on this unique family of insects is planned for the future.

Ursinus College
Collegeville, Pennsylvania

OBSERVATIONS ON THE NATURAL HISTORY OF THE COMMON MUSK TURTLE, *STERNOTHERUS ODORATUS* (LATREILLE) *

PAUL L. RISLEY

INTRODUCTION

"To tell American students that little is known of the habits of Turtles, the laying of their eggs, the growth of their young, etc., would perhaps excite a smile in those, who, as boys, have been in the habit of collecting Turtle's eggs, egg-hunting being an occupation of which boys are fond the world over. Yet so it is: what every inhabitant of the country may have seen again and again has not yet been collected in scientific works." — Louis Agassiz, 1857.

IT DOUBTLESS would be difficult for Agassiz, were he here at the present moment, to believe that his statement of 1857 has remained true for nearly seventy-five years. Nevertheless, as Babcock (1919) has written, "The same conditions, although to a far less extent, still exist. . . ." Much information concerning the natural history of most of the turtles of the world is still to be compiled and recorded, in spite of the extensive monographs by Agassiz and Babcock on these interesting animals. It is not my intention to attempt a collection of the facts presented in the literature on the natural history and habits of turtles in general. I wish, rather, to add some significant observations to the data available concerning the habits and life-history of one species, namely, the common musk turtle, *Sternotherus odoratus* (Latreille), known in some localities as the "stink-pot terrapin" and in others as the "little snapper." This paper gives the results obtained from incidental observations made in connection with studies on the development of this species, and they

* Contribution from the Department of Zoölogy, University of Michigan.

seem worthy of record — especially so, since the small amount of information found in the literature is widely scattered, is sometimes erroneous, and, in many instances, requires confirmation.

GENERAL CONSIDERATIONS

The musk turtle, *Sternotherus odoratus* (Latreille), occurs in great numbers in the region about Ann Arbor, Michigan, especially in the many and easily accessible fresh-water lakes. The majority of these observations were made at Whitmore Lake, an inland lake about twelve miles north of Ann Arbor. Additional materials were obtained from other lakes, including Pleasant, Portage, and Base-line, as well as from the Huron River.

The species is widely distributed and is generally abundant. Its range extends from southern Canada south to the Gulf of Mexico and west to Illinois and Wisconsin in the northern part and to Texas in the southern (Ditmars, 1907).

General descriptions of *Sternotherus* have been given in numerous places in the literature and need not be repeated here. The reader is referred to Ruthven, Thompson, and Gaige (1928) for a complete taxonomic description of the species here described. The carapace is oval in outline and is considerably arched. The plastron does not nearly fill the opening of the carapace, and is narrow, short, rounded anteriorly, and emarginate posteriorly. The anterior part of the plastron is slightly movable on a transverse hinge between the abdominal and the pectoral scutes. Areas of skin separate all the plastral scutes of the adult. The neck is long and the head large, with a conical, tapering snout. The skin is soft and covered with numerous fleshy papillae. There are two or more pairs of barbels or enlarged papillae on the chin and the throat. The coloration is of a dull brownish or olive tint, sometimes marbled or mottled with lighter olive or brownish yellow. Gadow (1920) states that "The only ornamental colouring is a pair of clear yellow broad lines on each side of the head, and a similar streak on each side of the lower jaw." The carapaces in the oldest and largest specimens I have seen have never exceeded 122 mm. in length.

The musk turtle received its common as well as its specific

name, *S. odoratus*, from the strong musky odor which it gives off when captured or handled. Babcock (1919) says: "A pair of inguinal glands secretes a disagreeable and penetrating odor of musk from which it derives its name." However, the odoriferous glands are not all in an inguinal position. I have been unable to find any in such a situation, and if they are there at all, they play a minor rôle in the secretion of the odor. Careful examination of a newly captured specimen from which the musky odor emanates reveals an orange or yellowish orange fluid along the border of the carapace at four separate and distinct places, two on each side. One gland is at each of the postero-lateral edges of the bridge, where it meets the carapace; another is on each side at the junction of the skin and the carapace, about midway between the anterior edge of the bridge and the cephalic end of the carapace. At each of these places a small white or yellowish pad of skin projects over the edge of the carapace, where it is usually possible to see the aperture of the duct which leads from the gland. These observations were made independently before I was aware that Dahlgren and Kepner (1908), who studied the musk glands of this turtle histologically, had already described their location. In an embryological study Stromsten (1917) describes their similar position in *Caretta caretta*. Morgan (1930) also confirms the description. Their statements make no reference to an inguinal position of musk-secreting glands in turtles. It is highly probable that there are no inguinal odoriferous glands in them, as there apparently are in some other reptiles, e.g. the alligator.

The musk turtle is strictly an aquatic form, being seldom found on land except during the egg-laying season. The thick, decaying vegetation in the shallow water along the shores of bayous affords an excellent hiding place and feeding ground. This turtle is often observed in the vicinity of muskrat houses, which are built mainly of the sedges that are abundant in these areas. Hay (1892) observes that "It appears to be disposed to frequent the deeper parts of ponds and small lakes, since in such places it is safer than about shores or on land." Newman (1906) believes that it goes into deeper water after the breeding season, since he could find no specimens during the summer months. However, I have been

able to find a certain number of specimens at all periods of the year, except in winter when the lakes are ice-covered. The number in shallow water is somewhat smaller during the summer season, but this is apparently a natural result due to increased activity during the warmer weather and to a wider range of distribution. There is probably no general change in habitat from the shallows during the breeding season to the deeper waters for the summer, that is, in the way of a uniform migration.

Hay further states that "They are often seen basking in the sun on some projecting rock or on some fallen tree, from which on the slightest alarm they drop off into the water." Newman, on the contrary, failed to observe musk turtles sunning themselves, as so many species of turtles are in the habit of doing. I have seen but two individuals under such conditions, and both of these were on fallen trees in the Huron River. When members of this species rest or sun themselves, they usually do so without leaving the water, for they are often found floating motionless on the surface, with only the top of the carapace visible. Newman has also observed this habit. He has encountered specimens of *S. odoratus* on land "at dusk, crawling about in the grass." The females are often seen on land during the egg-laying season, and especially toward evening. Occasionally individuals of both sexes have been captured while they were crossing highways which border lakes; such land excursions, however, are apparently infrequent. Babcock (1919) also indicates that "This animal is strictly aquatic in its habits, seldom, if ever, leaving the water, except to deposit its eggs; hence, it is not commonly known." Their habit of remaining in the water and in hiding has concealed them from many of their enemies, as well as from the observations of man. The species is, however, one of the most abundant.

HIBERNATION

In the winter, when the musk turtle is inactive, it probably buries itself in the mud beneath heavy vegetation. Babcock (1919) says that "Upon the approach of cold weather, it burrows into the mud and hibernates until spring." The close association of this turtle with the habitat of the muskrat suggests that musk-

rat holes and burrows might offer excellent hibernating conditions. Wetmore and Harper (1917) report the discovery of a specimen of *Kinosternon pennsylvanicum* (Bose) immediately after its emergence from hibernation on land. It was covered with freshly dried earth, and a search resulted in the discovery of a burrow beneath a dense growth of smilax. This burrow was about 9.5 inches deep, large enough to allow the turtle to enter without difficulty. They write: "Several fresh shells of *Aromechelys* (*Sternotherus*) *odoratus* and one or two of *Kinosternon pennsylvanicum* were seen lying about in wooded areas bordering this same marsh. Thus the emergence of these turtles had been of interest to others." This statement apparently implies that *S. odoratus* may also hibernate on land. Information on the subject of hibernation of turtles appears to be inadequate and somewhat fragmentary. It is difficult to make observations upon hibernating turtles in nature, and also in the laboratory. Numerous statements in the literature only indicate the probability that the turtles bury themselves in the mud during the winter months, or in burrows on land, and, in the case of *Cistudo*, under decaying materials (Gadow, 1920; Rollinat, 1899).

In the early spring the animals may be captured with a net by scooping up a few inches of mud and débris from lake bottoms. They are usually in shallow regions where the water is from one to two feet in depth. When discovered in this manner they are very inactive, and the heads and legs are drawn well up into the shells. The carapaces at this time are usually covered with thick growths of algae. In most of them these coverings disappear as the season progresses and as they become more active. The green color of the algae is of material advantage to them, since it serves as a camouflage when they are in the water. The disappearance of the algae may be due to a shedding of the horny scutes to which they are attached, or it may be the result of constant friction of the carapace against the weeds and sticks among which the turtles are moving. That the scutes are shed at odd times is a certainty, but whether or not this occurs regularly each spring is unknown. Animals kept in the laboratory always exhibit this moulting or sloughing of the horny scutes of the plastron

and carapace. In nature, the scutes may be found along the lake shores and also in the water.

The earliest dates of collection were March 25, 1928, and March 23, 1929. Both sexes probably emerge from hibernation at about the same time, although the early collections show a larger number of males. This might indicate that the males appear somewhat earlier than the females. Young animals make their appearance about a month later, near the first of May.

SEX RATIO

In the spring of 1930 a series of collections of adult specimens was made in an effort to obtain data on the sex ratio in this form. An examination of 255 individuals showed a large predominance of females, which outnumbered the males in a ratio of 1.0 to 2.3. The materials from which the figures are taken are presented in Table I. If the collections which were made after the breeding season (May 20, 1930) are omitted, the 161 animals taken earlier in the spring show an excess of females in a ratio of 1.0 to 1.65. The number is small, but the figures may have some value, since so little is known concerning the sex ratio of animals in nature and of those used infrequently in genetic studies.

At the United States Fisheries Biological Station at Beaufort, North Carolina, Hildebrand (1929) has found that in the diamond-back terrapin (*Malaclemmys centrata* and *M. pileata*) the males are fewer than the females in a ratio of 1.0 to 4.4. This is a striking deviation from the expected sex ratio of 1 to 1, but the numerical difference exists in both selected and unselected lots at the terrapin breeding farm. Since the sex of young individuals cannot be determined by external characters until a length of about three inches has been attained, no data on the sex ratio were obtained from newly hatched animals. If a 1 to 1 sex ratio occurs in the young terrapins, it seems probable that numerous males fail to reach maturity because of a high mortality rate. Hildebrand concludes that "Such a supposition does not appear to be tenable, however, because the number of deaths in some of the lots was too few, even if males only had died, to make a ratio of 1 to 1."

These are the only statements in the literature concerning the sex ratio of turtles, and it is interesting to note that they both indicate a dominance of the female sex.

TABLE I

DATA ON SEX RATIO OF *S. ODORATUS* (LATREILLE)

Date of collection	No. of specimens	Males	Females
MICHIGAN, 1930			
Whitmore Lake			
April 25	2	1	1
" 29	7	2	5
" 30	8	4	4
May 4	79	31	48
" 11	2	1	1
" 14	49	19	30
" 25	5	2	3
" 30	30	5	25
June 14	59	9	50
Silver Lake			
May 3	14	3	11
TOTALS	255	77	178

BREEDING HABITS

Throughout the spring both sexes are found in the same areas, and they are closely associated until the middle or latter part of May, after which the males apparently begin to disperse (Table I). The females remain in the shallow areas near the shores until their eggs are deposited, when they, too, leave the breeding grounds. As many as thirty specimens have been taken within a radius of fifteen feet. Hallowell (1856) reports that 259 individuals have been taken from a single hole; this was in Pennsylvania. The close association of the sexes during the month of April and the early part of May is taken as an indication that mating occurs during that period. Unfortunately, I have been unable to make any actual observations of mating pairs. Numerous individuals have been kept in the laboratory during this

period and have been carefully watched with the hope that the courting and mating activities might be observed. Several times I have come upon a pair which were apparently mating, but these were below the surface of the water. Upon being disturbed, however, they immediately broke away from each other, so that no observations of copulation could be made. During copulation the plastron of the male is superimposed upon the carapace of the female, but no further details of the mating can be given. In the field, as well as in the laboratory, numerous individuals have been observed in their courting activities. The males are the aggressors, continually following the females about. So far as I can determine, there are no data on record on the copulation of this species. Cunningham (1922) has presented some information concerning this act in *Chrysemys cinerea*, and Morgan (1930) in *Clemmys insculpta*, but these seem to be the only available references on mating of turtles.

The fact that the eggs are first found in the oviducts about the middle of May indicates that mating activities are concluded for the season at that time. Furthermore, testes taken from males during the latter part of May show the beginning of a new spermatogenetic cycle and of what seems to be a degeneration of spermatozoa. The latter condition, however, requires further investigation. The number of spermatozoa, normally stored in the epididymis and in the seminiferous tubules of the testis, is greatly reduced, and the testis and epididymis have reached a minimal size by the latter days of May. Motile spermatozoa are found in the oviducts of the females, even in summer following egg-laying. Barney (1921) segregated ten female diamond-back terrapins from males. They continued to produce fertile eggs for four successive years. This is apparently one of the longest periods during which spermatozoa have been known to live and remain functional in vertebrates. It is on record that the sperm introduced into the oviducts of bats, certain snakes, and some salamanders remain functional for as long as a year, but in chickens they will fertilize eggs for only the next twenty days following copulation (Marshall, 1922).

In the oviducts of all females of the musk turtle examined

during the period following emergence from hibernation there were great numbers of motile sperm. It seems improbable that copulation could occur during hibernation, since the animals are extremely inactive at that time. Accordingly, mating had already occurred either in the spring of the year after emergence or at some time the year before, possibly in the fall or late in the summer, and the sperm had remained alive and functional in the oviducts throughout the winter. If the latter alternative is true, as stated by Agassiz (1857) and Evermann and Clark (1920), it seems probable that mating occurs in both the spring and the fall. During the summer the number of mature sperm is reduced in the males, and the new spermatogenetic cycle is not completed until the latter part of August. The time of breeding is apparently closely associated with, and may be dependent upon, the condition of the male sex glands. Rollinat (1899) records the following interesting observations on the breeding habits of *Cistudo europaea* (Dum. et Bibr.): "Les mâles sont en rut pendant presque toute l'année. Sauf en décembre et janvier, j'ai vu des mâles fixés sur des femelles pendant tous les autres mois, même au commencement et à la fin de l'hivernage, car cette Tortue hiverne aussi bien dans la terre ou le fumier; j'ai souvent observé plusieurs mâles superposés sur la même femelle! J'ai eu à déplorer bien des fois la mort de femelles noyées par des mâles qui les fatiguaient en restant plusieurs jours fixés sur elles; des mâles furent noyés par des individus du même sexe!" Mating is probably resumed in the spring at the point at which the onset of winter interrupted it in the preceding fall. It seems certain that mating does occur each spring at some time before ovulation and the entrance of the ova into the oviducts, although it obviously is not necessary for the annual production of fertile eggs, as shown by Barney's experiments.

Ovulation usually occurs between the 15th and the 20th of May. I have never observed a second period of ovulation, or of egg-laying, in a single year. Some species of turtles may produce two sets of eggs a year (Gadow, 1920), but *S. odoratus* is not one of these. Although many specimens have been examined before and between these dates, I have never seen a single egg in the

oviduct which did not have the shell membrane and some albumen already laid down; nor have I ever seen an ovum in the abdominal cavity immediately after ovulation. The eggs remain in the oviducts for a period of from twenty to thirty-five days, after which they are usually laid; this is the normal length of time required for the secretion of the albumen and the shell. At the same time it is interesting to note that embryonic development is retarded while the egg remains in the oviduct, so that at the time of laying the embryo is in an early stage of gastrulation. The rate of cleavage is extremely slow in comparison with that in other vertebrates. Twenty days or more are required for the embryo to complete the cleavage stages.

Under extreme conditions eggs may be retained in the oviducts for extended periods. Agassiz (1857) reports a case in which only one egg was deposited, in the middle of July. Some specimens which I kept in the laboratory did not deposit their eggs until the first of August, when only one or two were laid instead of the usual three or four. These were opened after a few days and the embryos were living, but in a very early stage of development. There is every indication that the developmental process would have continued had they not been opened and had the embryos not been killed. One specimen apparently did not deposit any of her eggs. She was released with others in the fall, and is believed to have been recaptured the following spring, although she had not been marked for identification. When this turtle was opened, three newly formed eggs were found in the oviducts, and three with intact shells and disintegrated contents were in the abdominal cavity. Only three empty follicles were in the ovaries, indicating that only three eggs had been produced that spring. If this condition was not caused by the retention of the specimen in the laboratory during the summer of the year before, and if it occurred under natural environmental conditions, it is of still more interest and significance. It implies a reversal of the normal direction of passage of eggs through the oviducts, a phenomenon heretofore unknown in turtles. The factors (reversal of ciliary motion in oviduct, anti-peristalsis, etc.) producing the reversal in direction are problematic.

Eggs were collected for the first time on June 10 in 1928; on June 7 in 1929; and on June 14 in 1930. Some had undoubtedly been laid a few days earlier, to judge from the degree of their development. In the summer of 1928 a female was discovered on the morning of July 17. She was on land, evidently seeking a spot to deposit her eggs. She was taken to the laboratory, where it was found upon dissection that the oviducts contained five eggs ready for deposition. This is the latest recorded date on which eggs ready for laying have been found in the oviducts of individuals of this species under normal conditions. Newman (1906) observed that eggs were deposited as late as June 25. The egg-laying season in this region may be considered to be during the last twenty days of June and the first five of July, during which period most of the eggs are deposited.

The number of eggs laid under normal conditions varies from two to seven, but is usually from three to five. Hay (1892) states that "They lay their eggs on shores in holes that they have dug in the sand with their hind feet. The eggs are from three to five in number, of an elongated elliptical shape, and have a hard smooth shell." Newman (1906) records that "Specimens were captured on land with eggs in the oviducts ready to be laid, on the following dates: June 11, 16, 20, 22, 23, and 25. In no case did I find more than three eggs in the oviducts. These were elliptical in form and nearly as large as the eggs of Chrysemys. The shell is hard and of a china-like consistency, brittle but capable of withstanding considerable pressure." Several specimens that I have examined have had more than three eggs in the oviducts. Two exceptionally large ones had seven and nine eggs. Clutches have been uncovered which contained two, three, four, five, and six eggs, but those with three to five are the most common.

Newman (1906) makes the following observations upon the nesting habits of *S. odoratus:* "On only one occasion did I have the good fortune to observe Sternotherus in the process of nesting. When I first encountered the little tortoise she was digging in some soft soil, using all four feet and her snout. On my approach she abandoned her work and wandered about for fully an hour trying different places. Finally, she selected for nesting a decayed

stump that had rotted down level with the ground. She dug with fore-feet and hind-feet a shallow hole about two inches wide and of about the same depth, and deposited two eggs therein. After covering these eggs with excavated débris, she went her way. The form and workmanship of this little nest were of an inferior order as compared with those of other species of tortoise I have observed." I have had the opportunity to observe several females in the act of nesting, which apparently may take place at any time of the day from early morning till twilight. None have been found nesting at night, although it is quite possible that they do so. Agassiz (1857) saw them laying at half-past eight in the evening. The nests I have seen in the sand were built in much the same manner as the one described by Newman and were of a similar type. They were on a sandy shore from about two to five yards away from the water, usually at the base of a tall weed or a clump of grass. Very often the eggs are not completely covered when the turtle leaves the spot of laying.

Eigenmann (1896) gives the following account of the egg-laying habits of *S. odoratus* at Turkey Lake, Indiana:

> The eggs are laid in the rotten wood on the tops of stumps standing in the margin of the lake. The turtles were frequently found in the tops of these stumps, and some of their eggs were wedged into the rotten wood as far as the finger could bore. Rotten logs removed some distance from the water are also favorable places for egg-laying, and in a mucky place of small area at the edge of the lake, 362 eggs were taken at one time. . . . While passing along a wheat field some turtles were seen coming from it, and on inspection it was found that they had deposited their eggs in depressions made by a cow while walking over the ground when it was soft. Still other eggs were found in bundles of rushes drifted together.
>
> An interesting change of habit seems to have taken place among these turtles during the past fifty years. Before that time the number of stumps standing in the margin of the lake must have been exceedingly small. The present large number is due to the rising of the lake after the building of the dam and the subsequent cutting down of the trees whose boles had become submerged. The habit of laying eggs in stumps cannot be of much more than fifty years' duration.

It would be interesting to determine whether this change of habit has occurred in other places under similar circumstances. I have also found numerous eggs in rushes that have drifted together along the shore.

The size of the eggs is variable, and apparently is dependent upon that of the female and the number of eggs laid (Fig. 78). For example, nine eggs removed from a very large female were all of minimum size, but three eggs removed from an average animal were of maximum size. Measurements were taken from a small

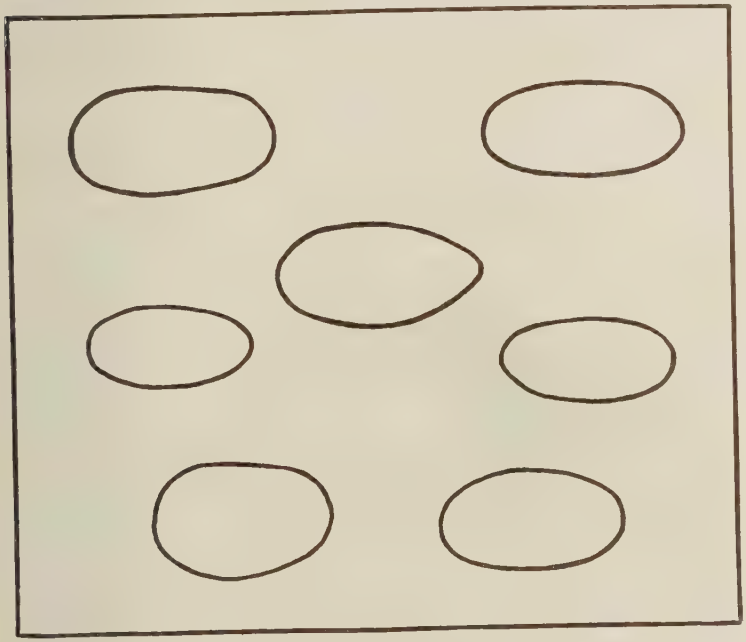

Fig. 78. Outline drawings of eggs of *S. odoratus* (Latreille), showing some variations in size and shape. × 1

lot of seventy-five eggs. The maximum length from tip to tip was 31.0 mm.; the minimum length, 24.0 mm.; the average, 27.1 mm. The maximum diameter of the eggs varied from 14.2 to 17.0 mm., averaging 15.5 mm. The variation in the size of the eggs also gives some index of the variation in the size of the young at hatching. Babcock (1919) says: "The young when newly hatched, are one-half inch long (length of carapace, which

is soft and pliable)." This figure, according to my results, seems much too small. Measurements made of two hundred specimens, which had been newly hatched from eggs kept in the laboratory, show the carapaces to be at least 19.0 mm. in length, to average 23.0 mm., and sometimes to reach even 25.0 mm. Babcock's specimens were apparently about one third smaller than mine. This is quite a variation, but, since Babcock's work was done in New England, it may be due to seasonal differences in different regions of the country.

The incubation period of the eggs of this species is also somewhat variable; however, embryos kept in the laboratory usually hatched in from sixty to seventy-five days after the eggs had been laid. This figure may be somewhat low, since the data were taken from embryos that had been kept in a room which occasionally reached a high temperature (37 degrees C.). Fluctuations in temperature and humidity play an important part in the regulation of the rate of development. This has been determined by direct observation. I have obtained many embryos during the summer, and when one is preparing a graded series of embryonic stages, slight changes in the growth rate are easily detected. At times the growth seems to be at a complete standstill; it has been noted that such modifications correspond to some direct change in the temperature or the amount of moisture in the incubating medium. During three summers the incubation period of eggs kept in the laboratory has fallen within the stated period. By keeping eggs in the basement of the laboratory, where the temperature rarely exceeded 25 degrees C., the incubation period was lengthened to approximately ninety days. Added moisture during the latter days of incubation delayed hatching until an optimum humidity was attained, but it also resulted in the death of numerous embryos. A number of eggs were collected from the natural environment on September 5, 1931. Some had already hatched, as evidenced by the broken shells, but no turtles were seen. They must have taken to the water near by, where the young are very well hidden from detection. Numerous eggs have been found in the spring; examination revealed the remains of embryos in them, but none of them were living. It seems that

the onset of cold weather may often interfere with the incubation period, prolonging it so much that the young never hatch; some turtles apparently pass the winter months in the egg and hatch in the spring (Gadow, 1920).

Favorite nesting places for the musk turtle are the houses of muskrats. Two houses examined on June 19, 1929, contained 196 and 253 eggs. One turtle was disturbed in the act of digging into a house, and another was on its nest. On June 10, 1928, 127 eggs were found in a single house; on June 17, 1928, one week later, the same house yielded 52 more eggs. Hankinson (1907) has pictured the eggs of the same species as he discovered them in a muskrat house at Walnut Lake, Michigan. A great number of the eggs laid on the shores and in the fields are dug up and eaten by foraging mammals, probably skunks, chipmunks, raccoons, and possibly others, although I have never personally observed the offenders. The tracks left near the nest are small, and are obviously those of some rodent. Their ability to find the turtle nests is quite remarkable, for very few eggs can be discovered after a nesting ground has once been visited by them. Only empty broken shells remain strewn around the neatly gouged-out nests. It seems likely that some birds, such as crows and herons, are also responsible for the destruction of some eggs. Both crows and herons have been observed on the tops of muskrat houses, which are often literally torn to pieces, in which case there are practically no eggs. Almost every house that is intact contains numerous eggs, whereas those which have been torn up by the birds have only a very few. They have probably been laid since the birds last raided the house, or have been overlooked. It is rather doubtful whether any land mammal would make excursions into the water for the express purpose of obtaining the eggs laid in the muskrat houses, and this makes it more probable that birds are the offenders in such instances.

HABITS AND FOOD

An examination of the stomach contents of numerous specimens shows that the species is a scavenger, and that it is omnivorous in its food habits. Newman (1906) has seen turtles feeding on land

snails, and he also states that they will eat anything given to them. Remains of fish, clams, snails, aquatic insects, and crabs, as well as much vegetable matter, such as buds of Elodea and other unidentified aquatic plants, have been found in their stomachs. Babcock (1919) says: "The Musk Turtle is principally carnivorous, feeding on small fish, aquatic insects, worms, fish eggs, pollywogs, and other small forms of animal life. It often takes the worm-baited hook of fishermen. One of my very small specimens (carapace length, $1\frac{1}{16}$ inches) attacked and devoured, whole and alive, an earthworm twice its length in exactly sixty-five seconds." Surface (1908) found snails, crickets, grasshoppers, larvae of Lepidoptera, and beetles in the stomachs of four specimens. I have used dried ant larvae, Elodea buds and leaves, earthworms, chopped liver, and beefsteak to feed young laboratory animals. They seem, however, to prefer live earthworms to anything else.

Babcock (1919) also records the following statements concerning habits of this turtle: "Its disposition is pugnacious and vicious, somewhat resembling that of the Snapping Turtle. It differs from the latter, however, in its method of snapping, for instead of quickly throwing out the head with a force that brings the whole body into play, it slowly stretches out its neck toward the object before snapping. The males are said to produce 'stridulating sounds' by rubbing together the patches of horny tubercles which occur on the hind legs, but I have never observed it." Gadow (1920) says that "It is mainly aquatic, and is one of the dullest and shyest species." It is most certainly dull, for a small amount of harmless teasing or rough treatment will induce it to turn its head about and bite itself severely. Its method of snapping is indicative of its cautiousness and shyness in attacking any object. The resemblance of its attitude to that of the snapping turtle is striking, and it is commonly known among fishermen of the region about Ann Arbor as the "little snapper," because of its pugnacious tendencies. In reality, it is quite harmless and easy to handle. As regards the "stridulating sounds" produced by the males, although I have heard such sounds coming from a laboratory aquarium which contained several musk turtles,

I have never been able to ascertain with any degree of certainty how they were produced, nor have I been able to determine that they were made only by the males. Babcock apparently obtained his information from Boulenger (1914), who states that "The back of the legs of the males in some of the species bears two patches of horny tubercles, and by rubbing these against one another stridulating sounds are produced very similar to those so well known in grasshoppers." The sounds may be produced in the manner suggested, but, on the other hand, they may be the result of some respiratory mechanism, similar to that in the alligator (Reese, 1931), or in other turtles (Gadow, 1920; Boulenger, 1914). Movements of the muscles of the throat that have been observed by the writer at the time of the sounds may be the responsible factor.

GROWTH AND AGE

Little is known about the growth rate of most turtles, and much of the available data has been derived from studies of growth under laboratory conditions, or in the terrapin farms (Hildebrand, 1929). It has been a popular belief that turtles are as slow in their growth as they are reputed to be in their motion, habits, and general metabolic activities. After presenting graphs showing the growth of the loggerhead turtle (*Caretta caretta* Linn.) over a period of four years, Parker (1926, 1929) concludes "that turtles, even large ones, may reach maturity at a comparatively rapid rate, and that the opinion commonly entertained of their great slowness of growth is scarcely justifiable. Without doubt their increase in late life is very slow and this may have given occasion for the belief in a low rate of growth in general."

In 1857 Agassiz gave the following growth chart for *Chrysemys picta:*

Year	Carapace length	Year	Carapace length
2	26.5 mm.	9 (♂)	74.0 mm.
3	42.0 mm.	10 (♂)	77.0 mm.
4	51.0 mm.	11 (♂)	80.0 mm.
5	54.0 mm.	14 (♀)	92.0 mm.
6	59.0 mm.	25 (♀)	121.0 mm.
7	66.0 mm.	Old (♀)	129.0 mm.
8 (♂)	72.5 mm.	Very old (♀)	163.0 mm.

The size given for the second year is that of the first spring after hatching, and the same relations are retained throughout the table given above. During the early years the rate of growth is very uniform, so that by the size differences only it is possible to arrange into sets of the same age younger specimens collected at the same time. Concentric lines of growth on the scutes indicate the number of years of age, and are valuable in confirmation of the size differences.

Pearse (1923) has shown that the western painted turtle, *Chrysemys cinerea* Bonnaterre, nearly doubles its length and weight during the second year of its life, increasing 73 per cent; during the third year, it increases 31 per cent; and during both the fourth and fifth years, 25 per cent. From this point on growth is slow, with an average increase of 5 per cent a year. An attempt was made by Pearse to correlate the size of this turtle with its age, but as Hubbs (1924) has pointed out, he neglected to indicate how the ages of the animals used were determined. Pearse, Lepkovsky, and Hintze (1925) studied the growth and the chemical composition of three species of turtles fed on rations of pure foods over periods of four and eleven months. This report, however, gives little information concerning the normal growth rate in natural environments.

Many of the data on growth of turtles have been compiled at the station for the culture of the diamond-back terrapin at Beaufort, North Carolina. Barney (1922) found that they may attain a length of from 130 to 150 mm. in four years, provided they are fed in winter. The same range of length was reached in six or seven years when they were allowed to hibernate. The maximum increase in length recorded by Barney was 81 mm. for a single year, and 104 mm. for two years. Hildebrand (1929) has recently completed a study of the growth of the same species. All the specimens were under direct observation for a period of from five to fifteen years. Variations in the growth of winter-fed and hibernating terrapins are discussed fully. There is a relatively slow growth after an age of from eight to ten years is reached. Whether specimens which are kept in captivity continually present the same conditions as those of a normal environment remains to be determined.

Agassiz (1857) says: "We find upon the surface of each scale, around a small angular plate [the plate of the first year's growth], a smaller or greater number of concentric stripes or regular annular rings, as they are exhibited on a transverse section of an old tree." It is possible to determine the age of young turtles by the number of the rings on the scutes. Coker (1920) has tabulated a series of measurements of diamond-back terrapins, and has been able to determine their ages by counting the annual rings. In his discussion of this method of age determination, he says:

> As the terrapin grows each scute extends its area peripherally and, commonly, in all directions. Thus with each period of growth, a ring of new tissue is added, separated from the central area (areola), or the preceding ring, by a line of depression. While these rings are spoken of as "concentric," the term must be taken with reservation, for growth is not equal in all directions. On the contrary, all scutes, except those of the anterior margin of the carapace and plastron, grow more anteriorly than posteriorly; hence, the rings are decidedly excentric, the center of each ring being (on most of the scutes) anterior to that of the preceding ring.

This same formation of growth rings occurs in *S. odoratus*. Certain difficulties, however, arise when attempts are made to calculate the age of a specimen in this manner. Coker has already pointed them out, as follows: (1) a more or less distinct line is produced by any cessation of growth, and by the resulting subdivision of each annual ring; (2) older shells become smooth through the repeated shedding of the horny layers; and (3) the growth of the older turtles is so slow that the rings are too small to be distinguished. Parker (1929) calls attention to the fact that early growth is subject to temporary cessation due to fluctuations in environmental conditions. After the musk turtle has passed its tenth year, it becomes almost impossible to determine its age by the ring criterion. Up to the age of ten years the method is reasonably accurate, but only in the cases of even younger specimens (two to seven years of age) can the age determination be made without some confusion. Benedetti (1925), in her study of the growth of *Testudo graeca*, was also able to determine only the age of younger specimens by counting the rings. Of 340 individuals used in her experiments, 94 could not be classified as to age on the basis of the number of annual rings. She concludes

that growth is not uniform, but that it varies with the seasons of the year, as, of course, would be expected. She finds also that growth varies with the size of the individual, as well as with the sex.

The oldest and largest members of *S. odoratus* seldom exceed 120 mm. in the length of the carapace. No sex differences are found in its length (Risley, 1930), as there are in numerous other species. As already stated, there is considerable variation in the size of the young at hatching (carapace length, 19.0 to 25.0 mm.). In 77 individuals, collected at large, it was possible to determine the number of rings on the scutes. These were found to form several definite age-groups, and measurements of the carapace length showed a corresponding arrangement into sets. The data have been plotted in the accompanying frequency curve (Fig. 79). The curve is based upon the average carapace length and the age of each group, and the variations are indicated. The variation within each group is not so great as would be expected if the variation at hatching were considered. Though the number of specimens available lessens the significance of the data considerably, I feel that the figures are not without importance. It is very difficult to discover the younger animals, and for that reason the number is small. Agassiz (1857) states that he hired a hundred men to hunt small turtles for him, but that, in a summer's work, they were unable to find a single one. In general, the data offer little that is new on the subject of growth of turtles, although they confirm the observations of Agassiz, Coker, Pearse, and others who have worked on other species. The figures do correlate the size of the turtle with its age, and therein find justification. I am confident that anyone can use these age-groups, and that, by calculating the carapace length and the number of rings on the scutes of the plastron and carapace, he will be able to state accurately the age of any specimen below the age of seven years; and that he will be reasonably certain of the age of the specimens from seven to ten years of age. The overlapping of the groups of the last three years considered may, however, cause difficulty. According to my observations, animals whose carapaces are of over 80.0 mm. in length are at least ten years old.

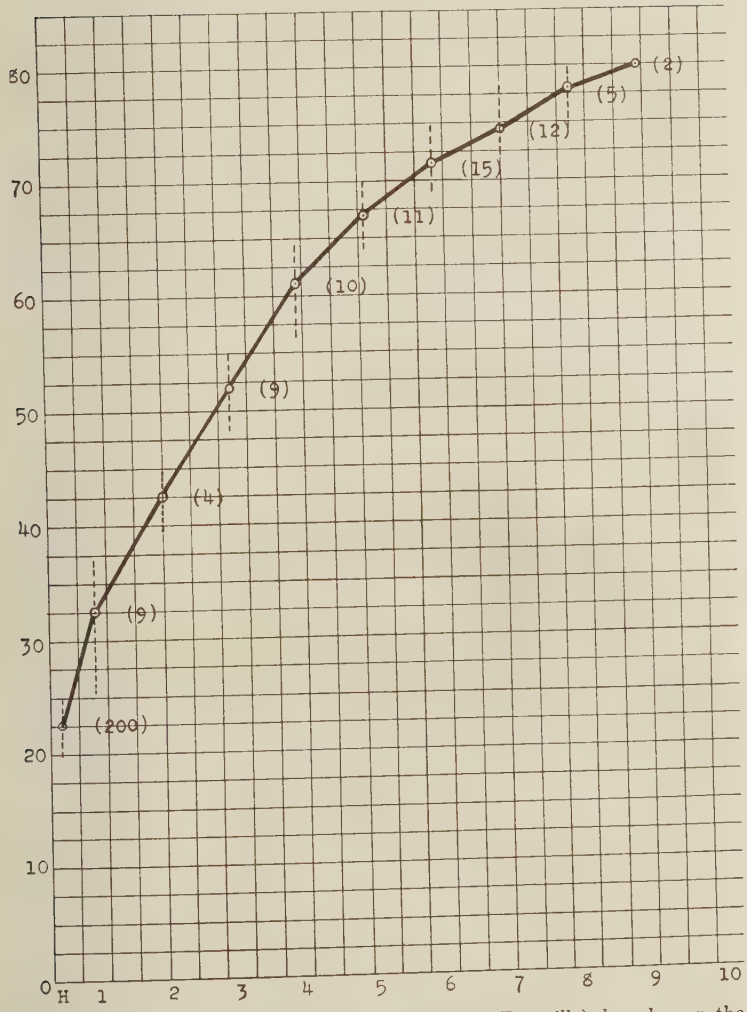

FIG. 79. Curve illustrating growth in *S. odoratus* (Latreille), based upon the carapace length in millimeters (ordinates) and the number of "annual rings" on the scutes (abscissae). The number of specimens in each group is indicated in the adjacent parentheses, e.g. (200). Vertical dotted lines show the variation within each group. The letter H signifies "at time of hatching." Numbers along abscissae correspond to each successive spring following hatching in September

ATTAINMENT OF SEXUAL MATURITY

The data on growth and age of *S. odoratus* were acquired primarily in an effort to determine the number of years which elapse before the turtles become sexually mature. Males and females of the musk turtle do not attain sexual maturity at the same age. An examination of testes and ovaries from the individuals used in the determination of the growth curve given above shows that the males produce motile spermatozoa from four to six years in advance of egg production by the females. If we base our determination of age on the data given in Figure 79, which correspond closely with unpublished data on the general growth of the gonads, the males become sexually mature in their third or fourth year — newly hatched individuals are considered as in their first year — but the females do not attain a size which allows the production of eggs until much later, from the ninth to the eleventh year. Agassiz (1857) states that *C. picta* does not lay eggs until the age of ten or eleven years, and Pearse (1923) agrees that this is the usual time of the first egg-laying by *C. cinerea.* Barney (1922) found that egg production by diamond-back terrapins, when they are fed during the winter, may begin as early as the fourth year, but that it usually begins in the fifth or sixth year. So far as can be determined, there is no other information available concerning the time when sexual maturity is reached by male turtles. It is singular that there should be such a striking difference (four to six years) in the ages of the males and the females when they first become sexually functional.

SEXUAL DIMORPHISM

At the time of hatching it is possible by dissection to be only relatively certain of the sex of a specimen. In order to determine the sex accurately, it is necessary to examine the gonads microscopically. It is impossible to distinguish the sexes by external characteristics until the third or the fourth year, as in the case of the diamond-back terrapin (Barney, 1922; Hildebrand, 1929). As stated above, there is no sexual dimorphism in the size of the bodies of the males and females, and no differences have been noted in the growth rate.

In a previous report (Risley, 1930) I have discussed in detail the anatomical characters which may be used in the identification of the sexes of adults of this species. The two characters which are generally applicable in the diagnosis of the sex of most chelonian species are also useful in *Sternotherus*. These characters are differences in the tail length and the concavity of the plastron. In the female the plastron is flat, very slightly concave, or slightly convex, and the tail is short, flattened laterally, and usually acutely pointed; in the male, the tail is much longer, circular in transverse section, and is capped by a blunt terminal nail, and the plastron is markedly concave. Besides these differences the skin around the anus of the female is covered with many fleshy, pointed tubercles, which are distinctly more numerous than in the males. On the dorsal side of the tail of the female there is, furthermore, a median longitudinal row of tubercles, which is absent in the males.

One of the most striking male sex characters is a double patch of compact, usually non-pigmented scales on the hind legs. These are situated on the median side of the knee joint, one patch on the distal surface of the thigh, and the other directly below on the proximal surface of the shank (see figures in original paper, 1930). They are present throughout the year and are not in any way correlated with the breeding season. They do not appear, however, until sexual maturity is reached, that is, until mature sperm are formed for the first time (third to fourth year of age).

The plastron is a variable character in the two sexes, not only with respect to its concavity in the males, but also in its size. The plastron of the female is longer in proportion to the length of the carapace than in the male. In the females the length of the plastron is usually above 72 per cent of the length of the carapace; in the males, it is usually below 70 per cent. A few individuals occasionally appear in which the percentage is between 70 and 72 per cent; they cannot be accurately identified by this character. The width of the bridge connecting the plastron with the carapace is also greater in the females than in the males. Another striking difference is the amount of skin which separates the plastral scutes. The exposed area is much wider in the males than in the females,

although there is some variation. Hallowell (1856) described certain sex differences in adults of *S. odoratus*, and also in some younger specimens. I have been unable, however, to confirm all the sex characteristics noted by him, and especially those given for the younger specimens, all of which were over three years of age.

SUMMARY AND CONCLUSIONS

The foregoing observations, made in the region about Ann Arbor, Michigan, have given the following data in regard to the natural history of *Sternotherus odoratus* (Latreille):

1. Emergence from hibernation usually occurs during the last week of March, with young animals appearing about one month later.

2. Data on the sex ratio indicate that the females somewhat outnumber the males.

3. Mating occurs in the spring between the approximate dates of April 1 and May 15; it may also occur in the fall. It appears that the time of mating is largely dependent upon the condition of the testes.

4. Ovulation takes place between the dates of May 15 and 20, and the eggs are normally retained in the oviducts for a period varying from twenty to thirty-five days, during which time the albumen and egg shell are secreted. Under normal conditions eggs are laid between the dates of June 10 and July 5, but this time is also subject to variation.

5. In the laboratory the incubation period of the eggs varies from sixty to seventy-five days after egg-laying. This appears to correspond favorably with the incubation time for eggs in a natural environment. The rate of development may be regulated by changes in the temperature and the humidity of the environment.

6. The number of eggs laid by a single turtle usually varies from three to six, but in exceptional cases as few as one or as many as nine may be produced. The number and the size of the eggs are closely correlated with the sizes of the females producing them.

7. An unusual case of prolonged retention of eggs in the ovi-

ducts, with their eventual retention in the coelomic cavity, is described.

8. Young individuals up to the age of seven years may be placed in year-groups on the basis of the length of the carapaces and the number of annual rings on the scutes of the carapaces and plastrons. Specimens from seven to ten years of age may be identified as such, but there always remains some uncertainty concerning the age determination. Above the age of ten years (carapace length, 80.0 mm.) the age cannot be determined by any known method.

9. Growth during the early years is relatively uniform for all specimens, but all are subject to temporary cessations due to environmental relations and seasonal changes. At first the animals apparently increase rapidly in size, and toward the tenth year there is a gradual slowing of the growth rate.

10. Sexual maturity is attained by males at the age of three or four years. Females mature later; they lay their first eggs between the ages of nine and eleven years.

ACKNOWLEDGMENTS

It is a pleasure to express my appreciation and thanks to Professor Peter O. Okkelberg of the Department of Zoölogy of the University of Michigan for his kindness and sincere encouragement and criticism during the progress of this study, which was undertaken at his suggestion.

The State University of Iowa
Iowa City, Iowa

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BIRDS OF KEWEENAW POINT, MICHIGAN

NORMAN A. WOOD

THE birds of the region of Keweenaw Point, Michigan, were studied by Dr. S. Kneeland, Jr., from August, 1856, to June, 1857, and a list of one hundred and forty-seven species was published in the *Proceedings of the Boston Society of Natural History*,[1] VI: 231–241. This region lies between 47° and 48° north latitude and between 88° and 90° longitude west from Greenwich. It is the so-called "copper region" of Lake Superior. Kneeland says: "It is possible that many birds, especially among the warblers and migratory species, will be added to this list hereafter. This district is, for the most part, heavily wooded with pines, spruces, firs, balsams, cedars, maples, and birches. The stillness of the dark and virgin forests is most remarkable." With one exception the writer found almost the same conditions there from April 22 to June 12, 1931. The big white pines had been cut for lumber fifty years or more ago, and small clearings have been made about Copper Harbor, Eagle River, and Eagle Harbor, and larger ones about Calumet, Hancock, and Houghton. This point was found to be an important spring migration route for many species from the south and southwest to Isle Royale and to points north into Canada. Most of the migrants fly to the end of this point, then six miles east to Manitou Island, the last resting place before crossing Lake Superior. Most of them pass to the east of Isle Royale, which is fifty miles west of Manitou, and out of the way for Canadian species. This was clearly shown by the flight of Raptores. From April 25 to May 6 thousands arrived at Manitou Island. Many rested there, but some kept on across to Canada without a stop, a flight of seventy-five miles or more. This flight was composed of large hawks: rough-legged,

[1] Boston, 1856–59.

red-tailed, red-shouldered, Cooper's, broad-winged, and one Swainson's, which was taken. No flight of these species was seen in the spring of 1930 at Isle Royale, and only one or two Cooper's and red-tailed were noted there. Sharp-shinned hawks were common; no doubt a few nested in the region, since they were present on June 12 at Copper Harbor. Snowy owls were common on Manitou Island, some of which remained during all of May. Several waves of migrating sparrows were seen, white-throated, white-crowned, and many Gambel's. One Harris sparrow was taken, but no others were seen. Song sparrows were abundant. Most of those taken were *M. juddi*, which form was found breeding on Isle Royale in 1930 and also at Copper Harbor in June, 1931. Few flocks of warblers were seen and only one or two individuals of many species.

Copper Harbor is a large, sheltered body of water, much of which is bordered on the north by an island and a long point of the mainland. The same name is applied to a small clearing which was surveyed and plotted as a town in 1853. It is now a summer resort, where a few good houses are the summer homes of people from Calumet. There is an excellent hotel, the Pontiac, with cottages to accommodate tourists and travelers.

ANNOTATED LIST

1. *Colymbus holboelli*. Holboell's grebe.

Only one bird was seen. On April 22, on the way from Calumet to Copper Harbor, a distance of thirty-five miles, the last ten of which were through ten inches of snow, I saw a grebe in the road, stopped the auto, and after a short chase ran the bird down. It was an adult male, in full breeding plumage. It was about a mile from the shore of Lake Superior.

2. *Colymbus auritus*. Horned grebe.

A rare migrant, or possibly a summer resident, since one pair was seen at Copper Harbor on June 9.

3. *Podilymbus podiceps.* Pied-billed grebe.

Not a common species here. Two were seen on Lake Fannie Hooe on April 25 and two or three days later.

4. *Gavia immer immer.* Common loon.

A common migrant and summer resident. It was seen at Copper Harbor from April 29 to June 12; a pair was observed several times on Lake Manganese.

5. *Larus argentatus smithsonianus.* Herring gull.

A rare summer resident at Copper Harbor, since only one pair was seen; they were observed almost daily about the Harbor. Near Portage Lake, on May 11, I saw one hundred or more feeding in a wet meadow.

6. *Mergus merganser americanus.* American merganser.

A common migrant but a rare summer resident; first seen on April 30, when fifty or more rested at Copper Harbor.

7. *Mergus serrator.* Red-breasted merganser.

A common migrant and summer resident; first noted on May 4, when a pair was seen on the Harbor; soon after a flock of thirty was counted. This flock was seen almost daily at this place, but only two or three were adult males.

8. *Anas rubripes tristis.* Common black duck.

A rare migrant and summer resident; the only pair seen was at Copper Harbor on May 21.

9. *Nyroca americana.* Redhead.

A rare migrant, since only three were seen on the Harbor; May 5.

10. *Nyroca valisineria.* Canvasback.

A rare migrant. Three were seen in the Harbor, on May 4, by the writer. Kneeland says: "This duck is occasionally seen here during its migrations, but I could not ascertain that any had ever been shot."

11. *Nyroca marila.* Greater scaup duck.

Not a common migrant, since it was noted only on May 27, when a flock of twenty rested in the Harbor.

12. *Nyroca affinis.* Lesser Scaup duck.

Not a common migrant; seen only on Lake Fannie Hooe a few times. On May 6 a female was shot from a flock of six, which was seen there until May 10. Kneeland does not list this species.

13. *Glaucionetta clangula americana.* American golden-eye.

Not a common migrant after April 24, when eight were seen at Copper Harbor. It was no doubt more common before my arrival.

14. *Charitonetta albeola.* Bufflehead.

Seven were seen on Lake Fannie Hooe on April 28, and a male in immature plumage was taken; a few were noted after May 24.

15. *Chen caerulescens.* Blue goose.

No doubt this is a rare migrant here. On April 28 two adult birds alighted on a wet meadow near the Harbor and allowed the writer to walk up to within ten rods of them before they flew. Dr. Kneeland does not mention this species.

16. *Botaurus lentiginosus.* American bittern.

A rare migrant or summer resident. The only one seen was at the west end of Copper Harbor on June 5.

17. *Coturnicops noveboracensis.* Yellow rail.

A rare migrant or summer resident. A fine adult male was taken at Copper Harbor by the writer on June 9. This is the first record of this species for the Upper Peninsula.

18. *Philohela minor.* American woodcock.

A very rare migrant or summer resident. The only one seen was at the edge of a willow thicket near the summer resort at Copper Harbor on May 15.

19. *Capello delicata.* Wilson's snipe.

This was a common migrant; first seen on May 6. On May 9, 10, and 11 numbers were feeding in a wet meadow near the Copper Harbor resort, but all had passed by May 12.

20. *Totanus melanoleucus.* Greater yellow-legs.

A rare migrant. Three were seen on May 11 and 12, but none were noted later.

21. *Tringa solitaria solitaria.* Eastern solitary sandpiper.

A rare migrant; first seen on May 11 at the west end of Lake Fannie Hooe, where one was taken on May 18. It was not seen later.

22. *Actitis macularia.* Spotted sandpiper.

A common migrant and summer resident. From May 4 on it was seen on the beaches of Copper Harbor and Lake Fannie Hooe. Sometimes there were six in a flock.

23. *Oxyechus vociferus vociferus.* Killdeer.

A common migrant and summer resident. It was seen daily after April 24. Two pairs nested near the resort at Copper Harbor.

24. *Bonasa umbellus togata.* Canada ruffed grouse.

A resident species, seen occasionally, but not so common as formerly. Sportsmen told me it had been abundant several years ago and then almost disappeared, but is now slowly increasing.

25. *Circus hudsonius.* Marsh hawk.

A rare migrant and summer resident. An immature male was taken on May 6, but only one or two were seen later.

26. *Accipiter velox velox.* Sharp-shinned hawk.

A common migrant and rare summer resident; first seen on April 24. It soon became common, and from May 5 to 17 hundreds passed over the resort, going east to Manitou Island, from which place they crossed Lake Superior to Canada.

27. *Accipiter cooperi.* Cooper's hawk.

A common migrant, but not so abundant as the sharp-shinned hawk. First seen on May 5, when it was migrating with other species.

28. *Astur atricapillus atricapillus.* Eastern goshawk.

A common migrant and rare summer resident. This species migrated in April, but one was seen in the forest south of Copper Harbor on May 16, where it no doubt bred.

29. *Buteo borealis borealis.* Eastern red-tailed hawk.

An abundant migrant, but a rare resident on the Point. It was first noted on May 4 among hundreds of hawks in migration, high up, going east.

30. *Buteo lineatus lineatus.* Northern red-shouldered hawk.

A common migrant and occasional resident. Many were seen in migration from May 1 to 5; also seen on May 23.

31. *Buteo swainsoni.* Swainson's hawk.

A rare straggler in Michigan. It was first taken in the state in October, 1883, by the writer, who collected the fourth in Keweenaw County on May 1, 1931. This is the only specimen taken in the spring in Michigan.

32. *Buteo platypterus platypterus.* Broad-winged hawk.

This common migrant and occasional summer resident was noted migrating with the great flight from May 1 to 6. One was taken on May 22 at Manitou Island.

33. *Archibuteo lagopus sancti-johannis.* American rough-legged hawk.

An abundant migrant. Hundreds passed over Copper Harbor from April 30 to May 6. These birds, like the other large hawks, were quite high and circled continuously to the east. According to the keeper of Manitou Light, many of these large hawks rested on this island before passing over Lake Superior.

34. *Haliaëtus leucocephalus leucocephalus.* Southern bald eagle.

A rare migrant and summer resident. One flying over Copper Harbor on April 23 was also seen several times in May and June at the same place, but no nest was found.

35. *Falco sparverius sparverius.* Eastern sparrow hawk.

A not common migrant or summer resident. It was first noted on May 4, when three were seen; others seen during all of May.

36. *Pandion haliaëtus carolinensis.* Osprey.

A rare migrant or summer resident. Only one was noted near the outlet of Lake Fannie Hooe on May 19, where it was seen again a few days later.

37. *Bubo virginianus virginianus.* Great horned owl.

A rare resident, not seen by the writer, but observed by a resident of Copper Harbor on May 29; a feather was picked up in a road near by.

38. *Nyctea nyctea.* Snowy owl.

A common migrant and winter resident. The only one seen by the writer was shot on Manitou Island on May 15 by the lighthouse keeper, who said there were others there during all of May.

39. *Megaceryle alcyon alcyon.* Eastern belted kingfisher.

A common summer resident; first seen on April 25 at Copper Harbor; others noted later at Lake Fannie Hooe and Manganese Lake, where a pair nested in May.

40. *Dryobates pubescens medianus.* Northern downy woodpecker.

A rare resident, first seen on April 23; observed but a very few times afterward.

41. *Sphyrapicus varius varius.* Yellow-bellied sapsucker.

A rare migrant and summer resident; first seen on April 23 at Copper Harbor, but not seen in May or June, although it no doubt nests in the hardwoods.

42. *Ceophloeus pileatus abieticola.* Northern pileated woodpecker.

A rare resident; the only specimen seen, an adult female, was observed at Fort Wilkins on May 22. Later one was heard drumming in pine woods near Lake Fannie Hooe.

43. *Melanerpes erythrocephalus.* Red-headed woodpecker.

A rare migrant and summer resident. First seen on May 11; observed only a few times later at the resort at Copper Harbor.

44. *Colaptes auratus luteus.* Northern flicker.

A common migrant, but rare summer resident. Several were seen on April 23 at Copper Harbor, but one or two were present almost daily through May to June 12.

45. *Antrostomus vociferus vociferus.* Eastern whippoorwill.

A rare summer resident, first seen on May 26 on road to Manganese Lake; seen and heard a few times later near Copper Harbor.

46. *Chordeiles minor minor.* Eastern nighthawk.

A rare migrant and summer resident. On June 1 the remains of one killed by a hawk were found in a road east of the state park, and one was seen near Copper Harbor on June 6 by the writer.

47. *Chaetura pelagica.* Chimney swift.

A rare summer resident; first seen at Copper Harbor on May 31. Some usually nested in the old chimneys of the houses at Fort Wilkins.

48. *Archilochus colubris.* Ruby-throated humming bird.

A rather common summer resident; first seen on May 27 at the resort on Copper Harbor; present almost daily in May and June.

49. *Tyrannus tyrannus.* Eastern kingbird.

A not common summer resident; first seen on May 19 in a clearing about the resort at Copper Harbor. A few were seen there later.

50. *Sayornis phoebe.* Eastern phoebe.

A rare summer resident; first seen at Copper Harbor on May 11; observed but a few times later.

51. *Nuttallornis mesoleucus.* Olive-sided flycatcher.

A rare migrant and summer resident; first seen on June 5, when a male was noted singing from the top of a tall spruce tree on the point north of Copper Harbor. No others were seen.

52. *Empidonax flaviventris.* Yellow-bellied flycatcher.

A rare migrant, or possibly a summer resident, since a pair taken on May 30 were mated. No others were seen.

53. *Empidonax trailli trailli.* Alder flycatcher.

A rare migrant or summer resident; first seen on May 29 in a tag alder (*A. incana* (L.) Moench) thicket. Only one seen later.

54. *Empidonax minimus.* Least flycatcher.

A common migrant and summer resident; first seen on May 26, but common in May and June.

55. *Otocoris alpestris praticola.* Prairie horned lark.

A rare migrant or summer resident. The only one seen was on a rocky beach at Copper Harbor on May 28. Kneeland lists it as "doubtful."

56. *Cyanocitta cristata cristata.* Northern blue jay.

A common migrant and summer resident. One was seen on May 23, another on May 26. This species became common on June 1, when flocks of from thirty to fifty were noted flying back and forth over the resort at Copper Harbor; they were observed as late as June 10.

57. *Corvus corax principalis.* Northern raven.

A rare resident, noted at Fort Wilkins on May 19, where two were seen. Another was seen May 22. Residents said this species was more common in winter.

58. *Corvus brachyrhynchos brachyrhynchos.* Eastern crow.

A common migrant and summer resident. Three were seen on April 22; a flock of twenty was seen on April 28. Later on larger flocks flew east over the Point.

59. *Molothrus ater ater.* Eastern cowbird.

Not common as a migrant or summer resident. It was first seen on May 4, feeding on the ground near some grazing horses.

60. *Agelaius phoeniceus phoeniceus.* Eastern redwing.

A rare migrant and summer resident; first seen on April 25; rare later.

61. *Sturnella magna magna.* Eastern meadow lark.

A rare migrant and summer resident. Two that were first seen were at the clearing on May 28. It never became common.

62. *Icterus galbula.* Baltimore oriole.

A very rare migrant and summer resident. The only one seen was observed on May 27. Not given in Dr. Kneeland's list.

63. *Euphagus carolinus.* Rusty blackbird.

A common migrant; first seen on April 23 at Copper Harbor. A flock of one hundred or more was seen on May 1 near Calumet.

64. *Quiscalus quiscula aeneus.* Bronzed grackle.

A common migrant and summer resident; first seen on May 4, when two were noted at the resort at Copper Harbor.

65. *Hesperiphona vespertina vespertina.* Eastern evening grosbeak.

A common migrant and not rare summer resident. Two were seen beside the road near Copper Harbor on April 22, and one was

observed at the west end of Lake Fannie Hooe on April 23. No more were seen in the region until June 6, when a flock of ten came to the resort and fed on the ground. An adult female taken had in her ovary one egg of the size of a large pea, and others smaller, but developed. On June 9 six more came to the resort, and another female was taken. This bird also had enlarged eggs in the ovary; there is no doubt that these birds were about to nest somewhere in the near vicinity. This species was found nesting in the same latitude in July, 1922, on Whitefish Point by J. S. Ligon.[2]

66. *Carpodacus purpureus purpureus.* Eastern purple finch.

A common migrant and summer resident; first seen on April 25, when two were noted. It did not become common until the middle of May, when males in the red plumage were first observed. Birds colored like the females were seen and heard singing; when sexed they proved to be males.

67. *Spinus tristis tristis.* Eastern goldfinch.

A common migrant and summer resident; first seen on May 26. It soon became common, and flocks fed on the dandelion seeds about the resort.

68. *Spinus pinus pinus.* Northern pine siskin.

A common migrant and summer resident. A flock of ten was seen near the resort on April 23. On April 29 three were noted picking up food on the ground near our log cabin. The last time one was seen in the region was on May 11.

69. *Passer domesticus domesticus.* English sparrow.

A common resident about the cities on the Point. It was seen at Hancock, Houghton, and Calumet, although none were noted at Copper Harbor. It was said by Mr. Beatty, the caretaker at Fort Wilkins, to occur there occasionally.

[2] *Auk*, 40: 314–316. 1923.

70. *Calcarius lapponicus lapponicus.* Lapland longspur.

A rare migrant in the spring of 1931; only two were seen. On May 11 one of a pair found in a large pasture near the resort was taken.

71. *Pooecetes gramineus gramineus.* Eastern vesper sparrow.

A common migrant and summer resident. Eight were seen at Copper Harbor on April 23; birds were noted nearly every day of our visit.

72. *Passerculus sandwichensis savanna.* Eastern savannah sparrow.

A common migrant, although not a common summer resident of the region worked, since there is little suitable habitat.

73. *Chondestes grammacus grammacus.* Eastern lark sparrow.

A rare migrant or straggler; but one was seen, on May 28, in the road near the resort. This is the first specimen from the Upper Peninsula, but Miss Mowbray reported it as "common at Marquette."

74. *Zonotrichia querula.* Harris's sparrow.

A rare migrant or straggler in Michigan. The writer collected his first specimen in this state on May 20. This bird, an adult female, was alone and was feeding on the ground a few feet from our cabin. This species has been recorded but a few times in Michigan: three times from the Upper Peninsula, once from Isle Royale, and two or three times from the Lower Peninsula.

75. *Zonotrichia leucophrys leucophrys.* White-crowned sparrow.

A common migrant; first seen at Copper Harbor, on May 11; noted until May 25, when all had passed.

76. *Zonotrichia leucophrys gambeli.* Gambel's sparrow.

Not rare as a migrant; first seen on May 16. It soon became as common as the white-crowned species, but, like it, was very shy and kept in the cover of the thick juniper bushes. It was not seen later than May 23. Barrows (1912) does not include this species in his lists of Michigan birds. It was first taken in the state on May 8 and 13, 1918, in Berrien County, by the writer. M. J. Magee of Sault Ste. Marie banded one in May, 1925, and took another on May 16, 1928, which he donated to the Museum of Zoölogy of the University of Michigan.

77. *Zonotrichia albicollis.* White-throated sparrow.

A common migrant and summer resident; first seen at Copper Harbor on May 4. Some nested in the region.

78. *Spizella arborea arborea.* Eastern tree sparrow.

A common migrant; at Copper Harbor on April 23 and 25. Not seen later.

79. *Spizella passerina passerina.* Eastern chipping sparrow.

An abundant migrant in flocks of from thirty to fifty from May 4 to May 25, and in pairs that were breeding after that date.

80. *Junco hyemalis hyemalis.* Slate-colored junco.

A common migrant and summer resident; first seen on April 23, when it occurred in flocks at Copper Harbor. Most of these had passed to the north by May 15. A few nested in the region.

81. *Melospiza melodia juddi.* Dakota song sparrow.

A very common migrant and also a summer resident. It was noted on April 23 and occurred in small flocks until May 15, when most of this species had passed to the north. In 1930

it was first seen on May 7 on Isle Royale, where all the song sparrows are of this form. A nest with five young was found by the writer on Smith Island, June 13, 1930.

82. *Melospiza lincolni lincolni.* Lincoln's sparrow.

A rare migrant or possibly a summer resident. The only one seen was taken on May 25 at the edge of a tag alder thicket at Copper Harbor.

83. *Melospiza georgiana.* Swamp sparrow.

A rare migrant or summer resident. The only one seen was taken on April 28 at the edge of a tag alder thicket at Copper Harbor.

84. *Passerella iliaca iliaca.* Eastern fox sparrow.

A rare migrant; seen first on April 24 near the resort at Copper Harbor, and again in open woods north of the Harbor on May 21.

85. *Hedymeles ludovicianus.* Rose-breasted grosbeak.

A rare migrant or summer resident. The only one seen was near the Copper Harbor resort on May 19.

86. *Petrochelidon albifrons.* Northern cliff swallow.

A common migrant and summer resident; first noted about Fort Wilkins on May 16. The writer was told by the caretaker, Mr. Beatty, that they nested there.

87. *Hirundo erythrogaster.* Barn swallow.

A common migrant and summer resident, first seen at Copper Harbor on May 4. Later two pairs nested in an old barn near by.

88. *Iridoprocne bicolor.* Tree swallow.

A common migrant and summer resident; first seen on May 13. Later a few nested.

89. *Riparia riparia riparia.* Bank swallow.

A common migrant and summer resident; first noted on May 18 near Lake Fannie Hooe.

90. *Bombycilla cedrorum.* Cedar waxwing.

An abundant migrant and common summer resident, but not seen until May 13, when two were noted at the resort at Copper Harbor. No others were seen until May 28; it did not become common until June 9 and 10, when flocks of from twenty-five to fifty appeared.

91. *Vireo olivaceus.* Red-eyed vireo.

A common migrant and summer resident; first seen on June 5 on the point north of Copper Harbor. This was the only species of vireo observed by the writer, but Dr. Kneeland lists the white-eyed vireo (no doubt a mistake).

92. *Mniotilta varia.* Black and white warbler.

A common migrant and summer resident; first noted at Copper Harbor on April 24, when two were seen in a pine-spruce forest near the resort. Dr. Kneeland does not include this species in his list; it was very scarce in 1931.

93. *Vermivora ruficapilla ruficapilla.* Nashville warbler.

A common migrant and summer resident; first noted on May 26 near the resort. This species is not listed by Dr. Kneeland; the writer found very few in the region.

94. *Vermivora celata celata.* Orange-crowned warbler.

A not rare migrant at Copper Harbor, where it was first seen on May 18 in a tamarack and tag alder swamp near the resort; a specimen was taken on May 25. It is not in Dr. Kneeland's list.

95. *Vermivora peregrina.* Tennessee warbler.

A migrant at Copper Harbor only. It was first seen on May 25; very rare in 1931, since the writer saw only two. It is not listed by Dr. Kneeland.

96. *Dendroica aestiva aestiva.* Eastern yellow warbler.

A common migrant and summer resident; first seen on May 19 near Manganese Lake. This species is listed by Dr. Kneeland.

97. *Dendroica coronata.* Myrtle warbler.

A common migrant and summer resident. It was first seen near the resort at Copper Harbor on May 9; flocks appeared during all of May. Pairs were seen in June, but no nests were found. This species is given in Dr. Kneeland's list.

98. *Dendroica magnolia.* Magnolia warbler.

A common migrant and summer resident; first seen on May 27; observed but few times later. This species is listed by Dr. Kneeland.

99. *Dendroica castanea.* Bay-breasted warbler.

Not a common migrant in 1931; a rare summer resident. The first one seen was near the resort in a tamarack tree on May 27; only one other noted. It is not listed by Dr. Kneeland, who does give the blackpoll.

100. *Dendroica fusca.* Blackburnian warbler.

A rare migrant and rare summer resident. The only one seen by the writer was near the edge of Copper Harbor in poplar trees. It is not in Dr. Kneeland's list.

101. *Dendroica virens virens.* Black-throated green warbler.

A common migrant and summer resident; first seen on May 27 in tamarack trees near the resort at Copper Harbor. Several were observed later by the writer; it is given in the list of Dr. Kneeland.

102. *Dendroica palmarum palmarum.* Western palm warbler.

This species was noted on May 13 and as late as May 28. It was the most common of all the warblers seen by the writer in 1931, but is not listed by Dr. Kneeland.

103. *Seiurus aurocapillus.* Oven-bird.

Not a common migrant or summer resident at Copper Harbor in 1931, since only two were seen, on May 15, on the point north of Copper Harbor.

104. *Seiurus noveboracensis notabilis.* Grinnell's water thrush.

A rare migrant at Copper Harbor. The only one noted was taken in a willow thicket near the resort on May 26. Not given by Dr. Kneeland in his list.

105. *Oporornis agilis.* Connecticut warbler.

A rare migrant, not a summer resident. On June 4 a male was seen singing in the top of a tall spruce tree on the point north of Copper Harbor. No others noted.

106. *Oporornis philadelphia.* Mourning warbler.

A rare migrant, not a summer resident; seen only once, on June 2, in a tag alder thicket near the resort.

107. *Wilsonia pusilla pusilla.* Wilson's warbler.

A common migrant and rare summer resident. It was first seen on May 26 in a tag alder thicket near the resort at Copper Harbor; several were noted later.

108. *Setophaga ruticilla.* American redstart.

A common migrant and summer resident; first seen on May 27 in tamarack trees near the resort at Copper Harbor; observed on June 8 in thick forest at the west end of the harbor.

109. *Anthus spinoletta rubescens.* American pipit.

A common migrant; first seen on May 15, when there was a flock of twenty in a wet meadow near the resort at Copper Harbor. This species is given in Dr. Kneeland's list.

110. *Dumetella carolinensis.* Catbird.

A rare migrant or summer resident. It was seen first on May 21 near the resort at Copper Harbor. No others were seen in 1931, but on Isle Royale the writer collected two on September 12, 1929. Dr. Kneeland says of this species: "This bird is not found at Portage Lake [Keweenaw County]."

111. *Troglodytes aëdon aëdon.* Eastern house wren.

A common migrant and summer resident. On May 29 a pair came to the resort and visited the boxes put up for them. Only two pairs were seen in the region.

112. *Nannus hiemalis hiemalis.* Eastern winter wren.

A common migrant and summer resident; first noted on June 2 near the resort at the side of a road near thick forest. Very scarce in 1931.

113. *Certhia familiaris americana.* Brown creeper.

A common migrant and summer resident; first seen on April 23 near the resort at Copper Harbor. It was quite rare in 1931.

114. *Sitta canadensis.* Red-breasted nuthatch.

A common migrant and summer resident; first seen on April 24. Several were noted later in May. Dr. Kneeland lists this species.

115. *Penthestes atricapillus atricapillus.* Black-capped chickadee.

A common resident, in winter and summer, but perhaps the birds seen here in the two seasons are not the same individuals. Dr. Kneeland lists the Hudsonian also, seen no doubt in winter, since in May, 1914, the writer observed a great number of this species migrate across to Canada from Whitefish Point, and in July found an adult and family of juveniles on the same Point.

116. *Corthylio calendula calendula.* Eastern ruby-crowned kinglet.

A common migrant, seen from May 4 to 21, when it left the region. Dr. Kneeland does not list either species of kinglet.

117. *Hylocichla minima aliciae.* Gray-cheeked thrush.

A rare migrant; seen only a few times. One was taken on May 27. Dr. Kneeland does not list this species, but does give Wilson's thrush and the wood thrush, neither of which was seen by the writer.

118. *Hylocichla ustulata swainsoni.* Olive-backed thrush.

A common migrant and summer resident, seen first on June 4 at Copper Harbor. This species was noted several times later; it is in Dr. Kneeland's list, as is the robin also.

119. *Hylocichla guttata faxoni.* Eastern hermit thrush.

A common migrant and summer resident; first seen on May 6, but observed several times later. It is not listed by Dr. Kneeland.

120. *Turdus migratorius migratorius.* Eastern robin.

A very common migrant and summer resident; it nests about the resort. First seen on April 22, but was doubtless there earlier. It is one of the most common species.

121. *Siala sialis sialis.* Eastern bluebird.

A common migrant and occasional summer resident, but was not seen at Copper Harbor until May 26, when a flock arrived. Later several flocks were seen. Dr. Kneeland does not list this species.

University of Michigan

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